Reconstructing the potential natural vegetation and soils of the high Andes

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ZUSAMMENFASSUNG

Da menschliche Aktivitäten Ökosysteme bereits auf vielfältige Weisen beeinflusst haben, ist es heutzutage fast unmöglich abzuschätzen, wie ein Ökosystem ohne anthropogenen Einfluss aussehen würde. Solche Basisdaten sind jedoch nicht nur wichtig um Rückschlüsse über die frühere Verbreitung und Zusammensetzung von Ökosystemen zu erhalten, sondern erlauben auch den menschlichen Einfluss auf Ökosysteme zu quantifizieren. In besorgniserregender Weise hat sich jedoch die Wahrnehmung, wie ein ungestörtes Ökosystem zusammengesetzt ist, in den letzten Jahren in Richtung anthropogen bereits gestörter Systeme verschoben. Ebenso sind quantitative Methoden, welche auf historischen Daten beruhen, oft weitreichender Kritik ausgesetzt. Nichtsdestotrotz beruhen die meisten Annahmen über den menschlichen Einfluss auf die Ökosysteme der Erde auf solchen historischen Daten, obwohl die Nachteile dieser Methode bekannt sind und sich oft nicht mit Erkenntnissen aus der ökologischen Forschung decken. Die ist besonders offensichtlich in den Puna-Graslandschaften der peruanischen Hochanden. Die grosse Ausdehnung dieser Grasgebiete, von Peru bis Argentinien wird oft als die natürliche Vegetation in diesem Gebiet angenommen. Auch in der Wissenschaft wird dies bis heute so vorausgesetzt, obwohl einst auch Wälder in diesem Gebiet vorkamen. Diese Wälder sind heute jedoch, abgesehen von einigen Relikten in schwer zugänglichen Gebieten, grösstenteils verschwunden. Der Rückgang dieser Wälder gibt nach wie vor Rätsel auf, wobei zum einen argumentiert wird, dass dieser Rückgang auf den Klimawandel zurückzuführen sei, zum anderen jedoch auch ein Rückgang aufgrund von menschlichem Einfluss nicht auszuschliessen ist. Diese Frage wird erst dann endgültig zu klären sein, wenn verlässliche Informationen über die natürliche Vegetation dieser Gebiete vorliegen.

Meine Forschung bietet eine neuartige Methode um die heutige, potentiell natürliche Vegetation abzuschätzen, frei von den Nachteilen subjektiver Meinung, unangemessener Experimentaldesigns und der schlechten Qualität und Anwendbarkeit historischer Umweltdaten zur Abschätzung der natürlichen Vegetation. Die einzigen Orte innerhalb der Puna-Vegetation, von denen angenommen werden kann das sie vom Menschen nicht beeinflusst wurden, befinden sich abgeschieden durch Steilklippen auf Felsplateaus, welche sie vor dem Einfluss von Vieh und durch Menschen verursachte Feuer geschützt haben. Diese Gebiete sind selbst heutzutage nur mit einer modernen Bergsteigerausrüstung und dem notwendigen Wissen zu erreichen. Eben diese Gebiete der peruanischen Bergketten des Urubamba und Vilcabamba nahe Cusco habe ich untersucht, um die natürliche Vegetation und die Bodentypen dieser Gebiete ohne den Einfluss von Menschen zu erforschen.

Um die Voraussagen meiner Forschungsarbeit zu bestätigen, zeige ich in Kapitel 1, dass die Vegetation auf Felsplateaus mit denen natürlicher Vegetation vergleichbar ist mittels Daten aus einem langjährigen Ausschlussexperiments, bei dem Weidetiere aus der Vegetation ausgeschlossen wurden.

In Kapitel 2 bestätige ich die Annahmen aus dem 1. Kapitel und kann zusätzlich zeigen dass unzugängliche Felsplateaus dazu genutzt werden können, die Entstehung von Böden unter dem langjährigen menschlichem Einfluss zu evaluieren, wobei dieser Einfluss gerade auf erhöhte Verwitterung jener Böden durch menschlichen Einfluss zurückzuführen ist. Durch diese Untersuchung war ich in der Lage, ein einheitliches Bezugssystem zu erstellen, welches auf positiver Rückkopplung zwischen menschlichem Einfluss auf die Vegetation, Bodenentstehung und der Akkumulation organischer Stoffe im Boden beruht.

In Kapitel 3 erweitere ich die Arbeiten der ersten Kapitel um 6 weitere Erkundungsgebiete und untersuche die ungestörte sowie gestörte Vegetation in diesen Gebieten unter Berücksichtigung von Fernerkundungsdaten, Daten epiphytischer Flechten und Waldstruktur. Aufgrund dieser Daten konnte ich die natürliche Vegetation dieser Gebiete bestimmen und feststellen, dass die ungestörte Vegetation sich hauptsächlich durch einen höheren Anteil an

Wäldern mit einer höheren Baumdichte, höheren Bäumen, sowie einen höheren Anteil an Totholz auszeichnet. Ebenso zeigt die natürliche Vegetation eine höhere Dichte krautiger Pflanzen, sowohl im Grasgebiet, wie auch in Wäldern. Erstaunlicherweise war die gefundene natürliche Vegetation reich an der Wissenschaft bisher unbekannten Arten. Einige dieser neuen Arten sind in Kapitel 6-8 beschrieben. Ebenso konnte ich herausfinden, dass die natürliche Vegetation eine hohe und einzigartige Diversität an Flechten aufwies, die sich hauptsächlich auf dem in der natürlichen Vegetation zahlreich vorhandenem Totholz finden liess, welches in von Menschen beeinflussten Gebieten nicht mehr zu finden ist, da es als Feuerholz gesammelt wird.

Der Einfluss des Menschen hat dramatische Auswirkungen auf die Eigenschaften von Ökosystemen, im speziellen bei der Umwandlung von Wäldern zu Grasland, wie auch bei der Degeneration von *Polylepis*-Wäldern. Ebenso wirkt sich der menschliche Einfluss auch extrem auf die Artenzusammensetzung dieser Habitate aus, insofern alle häufigen Arten ungestörter Vegetation in gestörter Vegetation fehlen. Während die lokalen Artenzahlen durchaus höher waren in Gebieten mit menschlichem Einfluss, waren die regionalen Artenzahlen jedoch durchaus geringer in diesen Gebieten. Dies lässt sich hauptsächlich darauf zurückführen, dass menschlicher Einfluss generalistische Arten bevorzugt und zu einer Homogenisierung der regionalen Arten-Zusammensetzung führt.

Entgegen der häufigen Annahme, dass Störungen durch Menschen die Fruchtbarkeit von Böden negativ beeinflusse, konnte ich keinen signifikanten Unterschied zwischen der natürlichen und der gestörten Vegetation feststellen im Bezug auf Bodenfruchtbarkeit. Die Art der Vegetation, welche auf diesen Böden gefunden werden kann, hat jedoch einen Einfluss auf die Boden-Fruchtbarkeit, was auf einen indirekten Zusammenhang zwischen menschlicher Aktivität und Bodenfruchtbarkeit hinweist. Durch eine Extrapolation dieser Ergebnisse auf das gesamte Untersuchungsgebiet konnte ich ebenso zeigen dass die Umwandlung der natürlichen Ökosysteme von Wäldern zu Grasland nicht zu einer geringeren Einlagerung organischen Kohlenstoffes geführt hat, da Böden in Grasgebieten mehr organischen Kohlenstoff speichern als das in Wäldern der Fall ist.

Kapitel 4 untersucht nicht nur den menschlichen Einfluss auf die Struktur von *Polylepis*-Wäldern, sondern auch die abiotischen Faktoren, die diese Wälder beeinflussen können. Sonnen-einstrahlung konnte dabei als wichtiger Faktor für die Höhe der Bäume aufgezeigt werden.

Während der Studien in diesen Gebieten wurden ebenso die höchsten Wälder und Epiphyten entdeckt (Kapitel 5), dies in Gebieten mit sehr viel niedrigerer Temperatur als vormals für die Baumgrenze angenommen wurde. Während der Studien in der ungestörten Vegetation wurden ebenso mehrere neue Arten entdeckt (Kapitel 9), wobei die wohl kleinste zweikeimblättrige Pflanze die faszinierendste Entdeckung unter diesen Arten darstellt (Kapitel 10). Diese Entdeckungen liefern uns bedeutende Hinweise über die Kapazität von Pflanzen, in unwirtlichen Lebensräumen zu überleben, mit weitreichenden Implikationen für das Studium von Baumgrenzen, weltweit.

Meine Studien zeigen, dass der Einfluss des Menschen zu weitreichenden Änderungen in Ökosystemen führen kann, jedoch solche Einflüsse nur schwer abzuschätzen sind in Unkenntnis der natürlichen Vegetation solcher Gebiete. Das Studium solcher ungestörten Ökosysteme ist daher unumgänglich, da vorher vollkommen unbekannte Eigenschaften solcher Systeme entdeckt werden können. Vorsicht ist daher angesagt wenn der Versuch unternommen wird, den Einfluss des Menschen zu evaluieren ohne genaue Kenntnisse der ungestörten Vegetation. Ohne diese Kenntnisse sind die Einflüsse des Menschen auf Ökosysteme kaum abzuschätzen.

SYNOPSIS

It is an indisputable fact that human activities are affecting properties and development of ecosystems to such a degree that it is, nowadays, almost impossible to get baseline values from undisturbed ecosystems. This baseline data is crucial for settling preconceived ideas of what is 'natural', whilst providing information on the extent of human impact, with far-reaching implications for our understanding of human influence on ecosystems, previous and current biodiversity distributions and paleoecology, to name but a few. Worryingly, current baselines are likely to be 'shifting' away from the true baseline as societal perception of what is natural becomes biased towards anthropogenically disturbed habitats whilst the use of historical ecological data to infer current baselines is fraught with criticism. Nevertheless, current understanding of human impact on Earth's ecosystems stems largely from paleoenvironmental proxies, despite the drawbacks associated with these methods, which has often created debate due to inconsistencies with ecological research. This is never more apparent than in the puna grasslands of the high Andes. These vast expanses of treeless grasslands, stretching from northern Peru to Argentina, are commonly considered the natural vegetation, with it still being unknown to many researchers that these high elevation landscapes once supported forests. These forests did, however, suffer a drastic decline to what is now seen today, with small relicts found only in highly inaccessible areas throughout the puna biome. The causes of this decline is the subject of current debate, with some attributing this to changing climate whilst others consider human impact to be the principal culprit. This debate will continue, with opinions regarding human impact on the puna biome remaining fundamentally biased or inconclusive, until we are able to obtain baseline data from pristine ecosystems.

My research provides a novel approach to infer real-time baselines based on current ecological conditions, free from the drawbacks associated with subjective observational studies, inadequate experimental studies, and the poor quality and applicability of paleoenvironmental proxies. The only places throughout the whole of the puna biome which can definitely be said to have not been affected by human influence are found on large crag ledges, isolated from livestock and the spread of human-induced ground fires. These ledges, which have deep soils and host a well-developed zonal vegetation, are inaccessible without mountaineering equipment or knowledge. I have accessed these pristine zonal ecosystems from the Cordilleras Urubamba and Vilcabamba, Cusco, Peru, to obtain baseline data on natural vegetation and soil parameters with which the cumulative effects of long-lasting and widespread human activity in the surrounding landscape could then be objectively assessed.

To validate the premise of my research, chapter 1 confirmed that inaccessible mountain ledges can be used to infer potential natural vegetation of the high Andean puna by showing how inaccessible zonal vegetation approximates undisturbed accessible vegetation from a long term grazing exclosure experiment. The exploratory study of chapter 2 provided further confirmation that inaccessible ledges can be used to infer natural soil development whilst evaluating the impact of long term human activity, whereupon this was seen to induce weathering in rangeland soils. Through this, a conceptual framework of positive feedback links between human-induced vegetation change, soil development and accumulation of soil organic matter was provided.

Chapter 3 then extends the study of pristine and disturbed vegetation and soil parameters over a further 6 large study sites, as well as including remote sensing data, lichen epiphyte data, and forest structure data from numerous pristine and disturbed forest stands. Upon analysis of this extensive baseline dataset, pristine vegetation was found to host a

greater proportion of forest, which was denser, with larger trees and more standing deadwood, as well as denser and taller herbaceous plant communities in both forests and grassland. Astonishingly, pristine vegetation was found to be largely comprised of new species to science and species with restricted range sizes, all of which lacked adaptations to human-induced burning and grazing. A few of these 'new' species were then described as part of taxonomic treatments in chapters 6–8. Pristine forests were also found to host a more highly diverse and unique lichen epiphyte flora specific to standing deadwood, which was plentiful in pristine forests but absent from disturbed forests due to firewood harvesting.

Human influence was seen to cause tremendous shifts in ecosystem properties, with large-scale conversion from forest to grassland, as well as human-induced degradation of *Polylepis* forest structure in the remaining stands accessible to humans (see also Chapter 4). Furthermore, human impact led to complete shifts in vegetation, with all species that are common to dominant in the pristine vegetation being completely lost in disturbed habitats. Although human disturbance was found to increase local species diversity, regional diversity suffered through the extirpations of ecological specialists. Furthermore, anthropogenic disturbance was found to benefit widespread and generalist species, which can actually proliferate through human-induced changes in the landscape, effectively leading to a homogenisation of the flora.

Contrary to belief that disturbance reduces soil fertility, soil nutrients and carbon were seen to vary insignificantly between pristine and disturbed habitats. Vegetation type was the main influence on soil parameters and so human impact on soils can be seen as indirect through human-induced vegetation change. Upon extrapolation of these results to the landscape level, differences in potential and current carbon stocks were not seen to be drastically affected by anthropogenic activity, despite large scale conversion of forest to grassland, because grassland has larger soil organic carbon stocks compared to forest.

Chapter 4 not only evaluated the detrimental effect of human disturbance on *Polylepis* stand structure, but also assessed the abiotic determinants of this structure, with solar irradiation found to be an important determinant of stand height. On studying pristine forest structure at very high elevations, we also documented the World's tallest highest elevation forests and highest vascular epiphytes (Chapter 5), as well as substantially lower temperatures for treelines than previously advocated. Whilst studying disturbed grassland vegetation for chapter 3, a few other discoveries were made of new species (Chapter 9), with the most fascinating being a minute dicotyledonous plant that is a contender for the World record of smallest dicot (Chapter 10). These discoveries will benefit our understanding of the physiological capacity of plants to survive in hostile environments whilst having implications for treeline ecology, with previous assertions over a general consistent global determinant of treeline positions needing reevaluation.

Studying pristine vegetation is crucial for gaining a better understanding of human influence on ecosystems whilst aiding our understanding of their general ecology as, with what has been shown here, previously unknown ecosystem properties and processes can be discovered. Our study highlights how human influence can cause both tremendous and benign shifts in ecosystem properties, with largely contrasting effects at local and landscape levels, but that these shifts are impossible to predict in the absence of baseline data. Caution should be taken when attempting to quantify anthropogenic perturbation on ecosystems in the absence of this baseline data as this research exemplifies how properties and processes forming natural ecosystems can be wholly unpredictable, and knowledge of human impact on ecosystem properties will be fundamentally biased, until we are able to obtain data from pristine ecosystems.

PROLOGUE

This project has combined my three great passions in life: botany, climbing, and my love of South America. From childhood, my dream has been to discover unexplored corners of the globe, like the famous 18th and 19th century explorers that I had always read about, and this PhD project has made that dream a reality. I hope that the reader is able to share in at least some of the excitement in exploring these untouched high Andean landscapes and the fascinating discoveries that were made.

THE QUESTION: ARE THE HIGH-ELEVATION ECOSYSTEMS OF THE ANDES NATURAL?

Human-mediated environmental changes have been noted on a global scale since the beginning of the Holocene with all continents, apart from Antarctica, having large-scale shifts in biodiversity documented (MacPhee & Marx 1997, Vitousek et al. 1997a; Lyons et al. 2004; Butchart et al. 2010; Kaplan et al. 2011; Govers et al. 2014). Research has attempted to elucidate the extent of anthropogenic impact and how the flora and fauna has evolved to cope with these added pressures (Vitousek et al. 1997b, Chapin III et al. 2000, Edwards et al. 2000, Ruddiman 2003, Ellis 2011, Zalasiewicz et al. 2011), but data relating to high mountain biomes remains scarce. Grass-dominated, treeless montane and alpine environments are commonly considered the natural vegetation of mountainous areas throughout the globe. This common notion has, however, been the subject of debate over centuries and, even with technological improvements, no consensus has yet been reached on how natural these environments actually are. Knowledge of the true natural state of these ecosystems is crucial, not only for settling preconceived ideas of what can be considered 'natural', but also for evaluating the extensity of human influence on these environments and the potential for ecosystem restoration, whilst gaining a better understanding of previous and current biodiversity distributions. Furthermore, the sheer size of high-elevation biomes, and the large influence they have on global atmospheric circulation (Shi et al. 2001; Duan & Wu 2005; Feddema et al. 2005; Jeffrey et al. 2012), means that any possibility that these landscapes are anthropogenically altered has wider implications when relating paleoclimatic feedbacks between land surface and climate.

Recent research has begun to suggest that early human activities, especially that of expanding Neolithic populations, could have had a fundamental impact on the vast majority of high mountain environments around the world, creating man-made landscapes with vegetation and soils very different to what would naturally occur (Kaplan et al. 2011; Ellis et al. 2013). Profound human-induced changes to high mountain ecosystems have been suggested for the high-altitude Himalayan biome (Miehe et al. 2009a) and adjacent Tibetan plateau (Miehe et al. 2009b, 2014), the Cordillera of New Guinea (Fairbairns et al. 2006; Hope 2009), the African afroalpine vegetation (Miehe & Miehe 1994; Wesche et al. 2000; Wesche 2002) and, of course, the European mountain ranges such as the Alps (Körner 2003). Amid much debate, this scenario has also been posited for the high Andean grasslands known as the puna (when dry) or paramo (when humid) (Ellenberg 1958; Laegaard 1992; Kessler 2002; White 2013).

The stereotypical view of the high Andes is that of extensive grasslands grazed by llamas and herded by Quechua or Aymara people. These high elevation grassland biomes are one of the global biodiversity hotspots and the most species rich tropical alpine habitat in the world, exhibiting twice the diversity than that of similar alpine vegetation in the Old World (Myers et al. 2000). Interestingly, as you walk through these expansive landscapes you will invariably notice small patches of trees in isolated difficult-to-access areas, well

above the closed timberline, which has raised doubts in many ecologists minds over the 'naturalness' of these grass-dominated landscapes. These forests constitute some of the world's highest treelines (Hoch & Körner 2005; Toivonen et al. 2011), with much research now focussing on these forests in order to decipher the limiting factors governing treeline positions (e.g. Bader & Ruitgen 2008; Wesche et al. 2008; Macek et al. 2009; Bader et al. 2014; Fajardo & Piper 2014). It remains unclear, however, whether the current position of these treelines is natural or whether a long history of human disturbance could have actually depressed the upper treeline.

The notion that these landscapes were once covered in woodland is still alien to many researchers (recent high impact publication, Rademaker et al. 2014, is a good example) but paleoecological studies do suggest that *Polylepis* forests once covered large areas of the central Andes, but suffered a widespread decline about 10,000 years ago (Hansen et al. 1984, 1994; Rodriguez & Behling 2012; White 2013). This forest decline has often been attributed to regional climate change, with the vast expanses of treeless, open grasslands and dwarf shrublands found throughout the high Andes being considered the natural vegetation. This view is based on palynological studies showing *Polylepis* woodland abundance to naturally fluctuate with there being no drastic declines in the last 5000 years, and authors discounting previous declines as too early to have been caused by humans (Paduano et al. 2003, van der Hammen & Hooghiemstra 2003, Gosling et al. 2009). Vegetation studies also show a high diversity of regionally endemic plants in grazed vegetation types (e.g. Koepcke 1961, Simpson 1986, Rauh 1988), and topographic relationships shown by forest patches (Bader & Ruitgen 2008) also support the idea that the current woodland distribution is natural. This has been challenged by other researchers on the basis of drawbacks in the palynological approach (see 'The task: obtaining baseline data' below), who have provided autecological evidence positing that much of the vegetation is man-made, with human activities being the culprit for the widespread vegetation changes observed (eg. Kessler 2002; White 2013; see below).

Humans are known to have been present at high elevation (>4,300 m.a.s.l.) puna sites of the Peruvian Andes since as far back as 12,800 years ago (Rademaker et al. 2014), just 2,000 years since the initial entry of humans to South America (Dillehay et al. 2008). The Andes are justifiably famous as a cradle of ancient civilization, witnessing the rise and fall of many societies over the past 12,000 years, with the Cusco region of southern Peru being particularly renowned for the presence and developments of pre-Incan civilisations that led to this region being considered the epicentre for Incan societal development (Burger 1992, Burns 1994, Kuentz et al. 2011).

However, it is disputed whether primitive hunters, early livestock farmers or nomads, likely to have been present in small numbers, were capable of causing this large-scale forest decline. Ellenberg (1958) was the first to suggest that the current patchy distribution of *Polylepis* woodland, which is now found as small relict stands in difficult to access areas, was due to human influence. These claims were initially heavily criticised (Koepcke 1961; Troll 1968; Simpson 1979, 1986; Rauh 1988) but, beginning in the 90's, a new wave of support for this theory began (eg. Becker 1988; Fjeldsa 1992a,b; Laegaard 1992; Kessler 1995a,b,c) with much ecological research beginning to focus on this subject.

Support for human involvement in this forest decline comes from autecological research which has found evidence that a large proportion of the Andes has conditions suitable for forest growth, but trees are only present in isolated areas inaccessible to humans or to the spread of human-induced ground fires (Hensen 1995; Kessler 1995c, 2000,

2002; Fjeldsa 2002; Kessler & Schmidt-Lebuhn 2006; Renison et al. 2006; Cierjacks et al. 2007; Coblentz & Keating 2008). Molecular studies have found both recent and historic evidence of forest fragmentation (Julio et al. 2008, 2009; Aragundi et al. 2011; Hensen et al. 2012; Quinteros-Casaverde et al. 2012; Gareca et al. 2013) whilst other studies have obtained direct evidence of the current detrimental effect of burning and grazing on forest growth and regeneration (Renison et al. 2002; Purcell & Brelsford 2004; Cierjacks et al. 2007, 2008; Giorgis et al. 2010; Marcora et al. 2013; Pollice et al. 2013). Palynological and pedological results, and associated ecological inferences based on soil profiles, from the adjacent paramo biome provide further support to the idea that nomadic people have greatly influenced the high-elevation vegetation of the central Andes by pastoralism and the burning and clearing of forests (White 2013).

Further support for a human influence on the high elevation puna ecosystem of southern Peru comes from other paleoecological research. Large-scale ecosystem degradation caused by pre-Incan agricultural activity has been suggested based on uncommonly large dust deposits encountered in ice-core analyses (Thompson et al. 1988). Palynological research from the Cusco region of southern Peru has also shown that pre-Incan civilizations had already encroached on the highest Andean landscapes and developed agricultural techniques which the Inca simply built upon (Kuentz et al. 2011, Mosblech et al. 2012). These civilizations developed a range of landscape-scale agricultural practises that reached into the highest ecological zones to support the growing populations of humans and their associated camelid grazers (llamas and alpacas) (Chepstow-Lusty et al. 2009).

Few publications are available on current human influence on the high elevation grassland environments of the puna and paramo. Most studies (e.g. Williamson et al. 1986, Keating 2000, Laegaard 1992, Hofstede et al. 1995, Cárdenas-Arévalo & Vargas-Ríos 2008, Valencia et al. 2013) have focussed on the more humid high elevation paramo grasslands of Ecuador and Colombia. Available literature on anthropogenic effects on the drier puna landscape of Peru is limited (Wilcox et al. 1987; Seibert & Menhofer 1992; Becerra 2006). The land use activities that are likely to have impacted, and continue to affect, these high mountain ecosystems are mainly pastoral practices, including the use of fire and logging (Tasser & Tappeiner 2002; Körner 2003; Ellenberg & Leuschner 2010; White 2013; Miehe et al. 2009a, b, 2014). Among these, grazing may appear least relevant, particularly as it is often considered as a natural component of many ecosystems where natural game have been present before the arrival of humans. However, the density of domestic animals in today's mountain ecosystems is usually much higher than that of natural grazers (Novaro et al. 2000; Kakzensky et al. 2008; Lichtenstein & Carmanchahi 2012). Similarly, while natural fires occur occasionally in many mountain ecosystems, humans often use fire on a yearly or bi-annual basis to, e.g., improve palatability of grasses (Laegaard 1992; Cochrane 2009). These two main activities, grazing and burning, are likely to have had a fundamental effect on the composition and structure of both the vegetation and soils of these environments with natural ecosystems being preserved in only the most inaccessible sites. This widespread anthropogenic impact has made it difficult to deduce what the natural vegetation should be in the high Andes.

There is thus an urgent need to provide baseline data so that the natural vegetation and anthropogenically affected environments can be analysed objectively to help settle debates over what is truly 'natural' whilst providing information on the extent of human impact and the potential for ecosystem restoration.

THE TASK: OBTAINING BASELINE DATA

In order to quantitatively assess anthropogenic influence on ecosystem development, it is fundamental to get "baselines" for natural plant diversity and composition, and soil genesis. Due to the virtual omnipresence of human activity in the Andes and elsewhere, pristine vegetation and soil are almost impossible to find and so researchers have used other strategies such as ecological inferences and historical ecological data. Both strategies are, however, imprecise, with fundamental drawbacks. Despite the widespread approval and usage of historical ecological data to infer present day baselines (Armstrong & Veteto 2015), the ecosystem properties that this data can infer are limited and, even with the few ecosystem properties that can be inferred, the quality and applicability of historical records used to make these inferences needs to be examined critically. The greatest criticism relates to the applicability of this approach, as precise knowledge on the composition of ecosystems millennia ago, before human impact began, would have only limited relevance on the reconstruction of present ecosystems which experience differing ecological conditions (Jackson & Hobbs 2009). The quality of historical records also suffers a number of limitations and drawbacks. The most widely used historical record for baseline ecological inference is the pollen record, although this is only limited to plants. Palynological inferences are hindered by a) an overrepresentation of taxa with windborne pollen, b) a lack of precision, with taxa only being identified to genus level and even this not being clear-cut, and c) the fact that pollen samples usually represent azonal vegetation (e.g. Cyperaceae swamp) because pollen cores are taken from lakes usually surrounded by wetlands. These drawbacks are never more apparent than when trying to infer a natural baseline vegetation for the high Andes, especially when focussing on the prevalence of woodlands in these high elevation ecosystems. *Polylepis* pollen is seen to have a very low dispersal rate, usually restricted to 700 m (Salgado-Labouriau 1979; Graf 1986; Kuentz et al. 2007), which has been corroborated by the majority of population genetic research on this genus (see Gareca et al. 2013 for an overall review), although studies by Schmidt-Lebuhn et al. (2007) and Hensen et al. (2011) suggest effective long distance dispersal for *Polylepis*! *Polylepis* species also do not grow anywhere close to wetlands, from which pollen cores are collected, with autecological studies already establishing that negative moisture balance and waterlogging are critical in determining the niche space available for *Polylepis* (Bader & Ruitgen 2008; Gosling et al. 2009). *Polylepis* pollen is also indistinguishable from *Acaena* pollen, a commonly encountered, closely related genus of herbs prevalent in disturbed humid puna grasslands (Kuentz et al. 2007). All these problems mean that inference of historical changes in woodland abundance need to be treated with caution and the idea of using this data to infer current baselines is ludicrous.

Thus, we need objective present day "baselines" for natural ecosystem (plant & soil) genesis. An approach that attempts to achieve this is that using experimental studies, most prominently grazing exclosures. However, this approach is hampered by slow ecosystem development (soil will take millennia and potential "climax" forest vegetation at least centuries) and, as soil conditions have already been changed by human interference, a different vegetation is likely to develop compared with the original natural one. Hence, the only option left is to conduct observational studies (e.g. Leuschner et al. 2009). However, even with this approach, ideal observational study sites are hard to find (therefore offering minimum replication as is true for the other approaches) and, more importantly, there remains a high uncertainty that selected "untouched" control sites are truly pristine. The majority of observational studies are flawed in their subjectivity, often being based on

researchers opinions of what is 'natural' which are invariably biased. A good example is that of Seibert & Menhofer (1992) who attempted to deduce the potential natural vegetation of the puna using a phytosociological approach comparing vegetation with differing levels of human disturbance. They lacked data on truly pristine vegetation and based their conclusions on the properties of natural puna ecosystems using their own opinion, with no objective dataset being used. Worryingly, current baselines are likely to be 'shifting' away from the true baseline as societal perception of what is natural becomes biased towards anthropogenically disturbed habitats (Pauly 1995; Papworth et al. 2009). Therefore, there is a need for ecological data from truly untouched ecosystems to objectively infer ecological baselines which has not, until now, been possible.

THE SOLUTION: INACCESSIBLE LEDGES

The basic premise of this doctoral research has been that remote mountain ledges, that are only accessible with modern mountaineering equipment, harbour relict patches of near-natural zonal ecosystems that can be used as an objective baseline to infer the natural Andean puna vegetation and soils. These inaccessible ledges were large enough to support zonal ecosystems (often several hectares in size; Fig. 1) and were not local microhabitats associated to steep rock faces. In comparison to the prevailing surrounding ecosystems, the human impact on the development of these inaccessible, pristine ecosystems could be

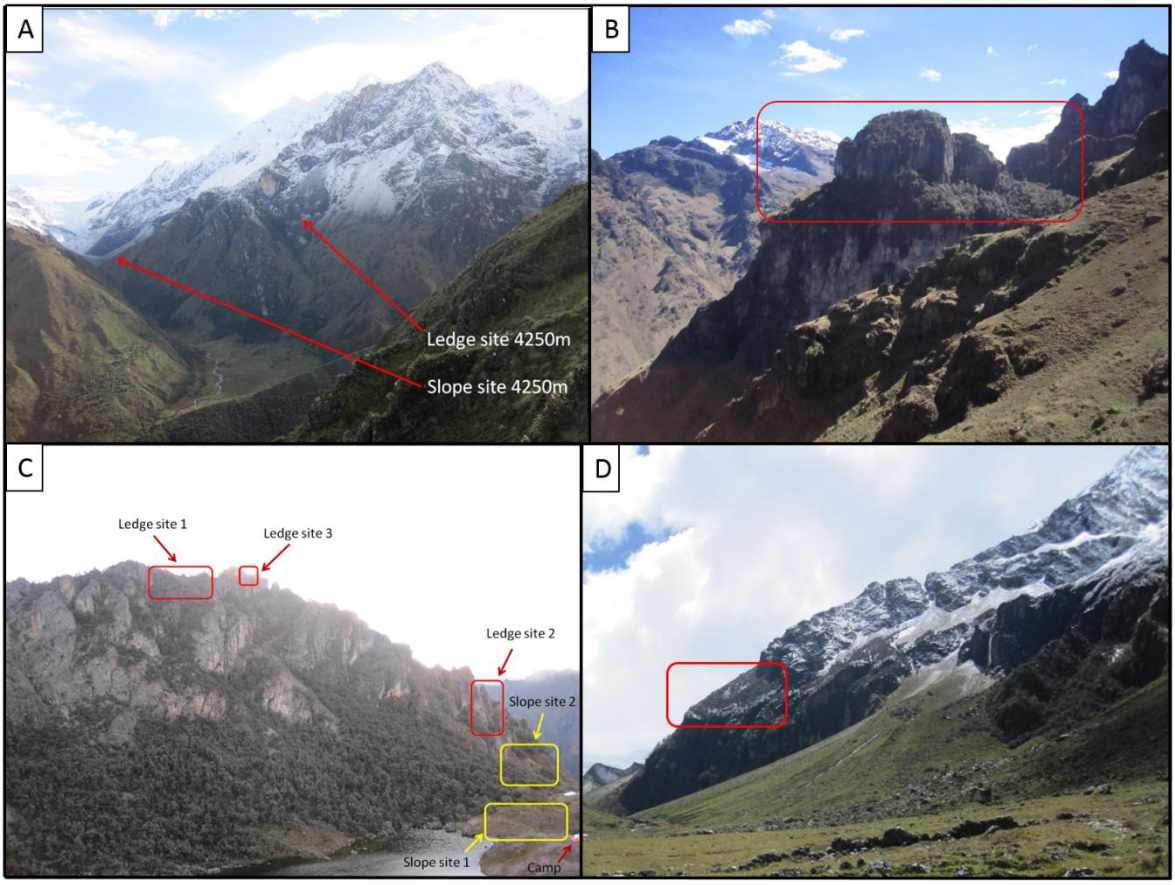

Fig. 1. *Some of the sites studied. A) Phacchaq valley, Cordillera Vilcabamba, showing the ledge and slope sites studied. B) The prominent tower known as Contorkayqu in the Valley of Huaran, Cordillera urubamba, showing the ledge sites studied. C) The mountain ridge alongside the Manalloqsa lake showing both ledge and slope sites studied. D) The Yanakaka ledge site, Cordillera Vilcabamba.*

directly withdrawn. To evaluate the impact of human influence on vegetation and soils, control sites on accessible slopes, as close as possible to the ledge sites and with similar abiotic conditions (e.g. elevation, aspect, climate) were also surveyed. According to the state factor model (Amundson and Jenny 1997), these have to be identical in climate, parent material, topography, age and differ only in biota (human impact through grazing).

With this method, we have obtained the first example of a present-day baseline, based on current ecological conditions, of vegetation and soil parameters, with some truly spectacular and unexpected results.

THE FINDINGS

To validate the premise of the overall project, i.e. that zonal vegetation on mountain ledges, only accessible using mountaineering equipment, can be used to infer the potential natural vegetation (PNV; Zerbe 1998) of the high Andes, the preliminary study of **chapter 1** was undertaken. In this study, I assessed differences in zonal vegetation between accessible and inaccessible sites inside and outside of one of the few conservation exclosures (i.e. long-term grazing exclosures) in place in the high elevation puna biome. The premise was that, if the vegetation in inaccessible ledge sites inside and outside of the conservation area shared similarities in composition and diversity with vegetation in accessible areas inside of the conservation area, then this proves, to a great extent, that zonal vegetation found on ledges can be used to infer the PNV of the study area. The results obtained did validate the overall premise of my research, with large similarities being found in vegetation composition and diversity between undisturbed areas, regardless of whether they were found on inaccessible ledges or accessible slopes. The PNV was found to be a distinct vegetation type with lower alpha diversity compared to adjacent disturbed habitats. These results were similar to the large-scale project (See chapter 3) but, at this stage, we were still cautious to announce that the PNV was dominated by new species to science as insufficient taxonomic work had been done. Thus, *Festuca proceroides* J.C. Ospina & S.P. Sylvester sp. nov., a dominant component of pristine areas, was left as *Festuca* aff. *procera* Kunth in this study.

In **chapter 2**, we conducted a preliminary study on the impact of anthropogenic disturbance on soil properties for one site in the Cordillera Urubamba, Cusco. We recorded soil and vegetation parameters from pristine forests and grasslands found on a large inaccessible ledge and compared these with nearby disturbed grassland, as no forests were present in accessible areas due to deforestation. The baseline data for pristine ecosystems highlighted an interesting scenario of long term human influence on soil development and accumulation of SOM whereby lower vegetation cover of soils, caused by long term grazing, increased soil surface temperatures and acidification resulting in increased weathering. High amounts of SOM, preserved through the formation of pedogenic oxides, also led to increased soil acidification whilst organo-mineral associations for SOM stabilization likely led to a higher degree of humification which, in turn, induced melanisation that increases soil surface temperatures. Thus, higher amounts of SOM caused higher soil surface temperatures and acidification that causes increased weathering. Combining all these findings, a conceptual framework of positive feedback links between human-induced vegetation change, soil development and accumulation of SOM was discovered. This study provided support for the overall premise of my research emphasising that “Using ‘inaccessibility’ as a tool to quantify human impact in future interdisciplinary studies may push research forward on evaluating anthropogenic impact on Earth’s ecosystems”.

Following on from this, **chapter 3** encompasses the entire research conducted during a three year field campaign from Aug 2010 – Aug 2013 in the Cordilleras Urubamba and Vilcabamba of the Cusco region of Peru. Eight large study areas, that included the sites covered in chapter 1 and chapter 2, were partitioned into different pristine and disturbed habitats and surveyed for their vegetation and soil properties. Numerous extra forest structure surveys were also done in other pristine sites throughout the two Cordilleras which were compared with surveys undertaken in disturbed forests by Toivonen et al. (2011). The findings were nothing less than spectacular.

It was fascinating, and completely unexpected, to find that the herbaceous layer of pristine vegetation was dominated by new species to science, with the vegetation also comprising rare species with restricted range sizes (Fig. 2B) and a highly diverse lichen epiphyte flora that was specific to deadwood substrate. Frighteningly, we found that human impact did not lead to slight shifts in vegetation composition but, rather, a complete shift with all dominant undescribed vascular plant species or species with short range sizes and lichen indicator species being completely lost. The resulting vegetation becomes occupied by widespread, broadly tolerant plants that are adapted to human disturbance, and which can benefit and proliferate because of this disturbance (Fig. 2A). This implies a homogenisation of the flora to favour a smaller subset of widespread plants which occupy a broad ecological niche and which can be successful in an anthropogenically impacted landscape. This has been implied before (eg. McKinney & Lockwood 1999), but these studies failed to find a decrease in beta diversity with increasing human impact meaning our results are one of the few examples (e.g. Harrison 1993) of the role of humans in reducing beta diversity and effectively homogenising the biosphere.

Natural vegetation structure was found to comprise a significantly higher proportion of woodland compared to disturbed, grass-dominated, landscapes with natural ecosystems containing greater biomass through denser forests, with larger trees, denser and taller herbaceous plant communities. Anthropogenic disturbance was seen to have a severe detrimental effect on forest ecosystems, reducing their overall cover at a landscape level whilst causing a deterioration of the remaining relicts that are accessible.

From these results it would be assumed that human impact on carbon stores would also be severe but, contrary to our expectations, we found there was only a relatively small difference when comparing potential and actual carbon stocks at a landscape level. This was largely due to soil organic carbon (SOC) stocks, which were the largest ecosystem carbon stock, being higher in grasslands compared to forests, whilst human impact had no direct effect on SOC stocks. Similar patterns were found for most other soil nutrient properties, implying that human influence on soils is only indirect through human-induced vegetation change, with the conversion of forests to grassland.

With this baseline now established, we show that natural ecosystems do not necessarily fit our preconceived ideas with previous assumptions regarding what is 'natural' needing to be reassessed. These differences from preconceived notions exemplifies how difficult it is to predict the true natural ecosystem state and that inferences of human impact on ecosystem properties will fundamentally be biased until we are able to assess real-time ecologically sound baselines. Our research also exemplifies the largely contrasting effects of human disturbance at local and landscape scales. At local scales, human influence can be seen to have relatively positive effects, creating higher alpha diversity through disturbance opening up many ecological niches whilst there being little effect on soil nutrients and overall carbon stocks. At the landscape scale, the picture is completely

different, with human influence seen to reduce regional plant diversity through homogenization and the loss of ecological specialists whilst causing massive changes in vegetation cover which influences soil properties and carbon stocks. Taking these differences into account, our study suggests that moderate levels of land use are likely to be compatible with biodiversity, soil and carbon conservation at the regional level.

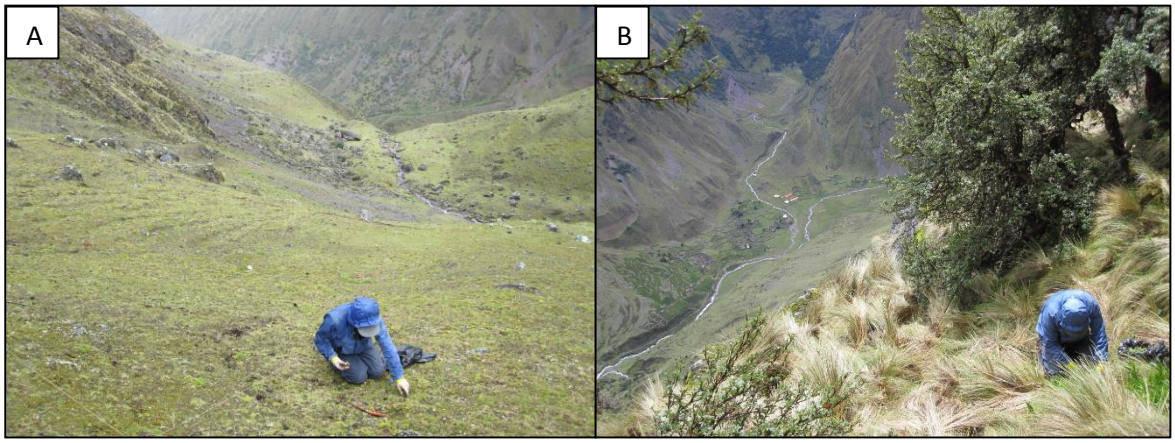

Fig. 2. *A) Example of a grazed accessible site consisting of a grassland of very low stature but high local species richness; B) Example of a nearby inaccessible site which contains the potential natural vegetation of the puna. Here, the vegetation is much less species rich and is dominated by undescribed species of tussock grass (*Calamagrostis sp. nov.1 *&* Festuca linigluma sp. nov.*) and trees (*Polylepis subsericans*).*

In **chapter 4**, we examined the effect of both human impact and climate on *Polylepis* tree height along elevational gradients in the Cordilleras Urubamba and Vilcabamba. Forest structure data from pristine forests was compared with that from accessible forests across different elevational bands in the two Cordilleras, with climatic data also being recorded from these sites. Our data showed that human disturbance inhibited trees from reaching their full potential height whilst pristine forests did reach their full natural height. Data from pristine forest stands also did not fit simple height-elevation models which predict tree height to linearly decrease with elevation. Instead, trees at high elevations were found to be incredibly large, giving them the World record of tallest high-elevation forests.

This research also provided important insights into the central topic in treeline ecology on what limits tree establishment, growth and survival at the upper boundary of forest growth. We found that differences in solar radiation received by sites was a major determinant on both tree height and the position of the upper treeline. Cloudier Cordillera Vilcabamba sites received less solar radiation resulting in lower temperatures at these sites and a resulting lower upper boundary and shorter forests compared to the sunnier Cordillera Urubamba. Furthermore, while it has been claimed that treelines globally correspond to a mean growth season temperature of about 6.7°C (Körner & Paulsen 2004, Körner 2012), our research along with other studies (Kessler & Hohnwald 1998, Bendix & Rafiqpoor 2001, Hertel & Wesche 2008, Cierjacks et al. 2008) suggest that Andean treelines formed by *Polylepis* may occur at substantially lower temperatures.

While conducting fieldwork studying forest structure at these treeline positions in the Cordillera Vilcabamba, fern epiphytes were noted to grow on *Polylepis* trees at much higher elevations than previously documented and led to the creation of **chapter 5**. Here we described a new World record for the highest elevation vascular epiphytes whilst also

documenting the climatic conditions at these sites with which we discussed the existing hypotheses on abiotic conditions limiting epiphytism. It was concluded that abiotic conditions at these sites were fairly amenable compared with what other vascular epiphytes endure in other parts of the globe and allows the postulation that, if these forests were to grow higher, these epiphytes would also be able to grow at even higher elevations with their elevational distribution effectively restricted by the availability of tree substrate.

During the entire field campaign a total of 2045 voucher specimens of vascular plant were collected with all but 10 being identified to species. Within these specimens, a total of 15 species were found to be undescribed 'new' species to science. The majority of these 'new' species were found associated with pristine vegetation (see chapters 1 and 3) and I endeavored to publish the descriptions as well as improve the taxonomic knowledge of these groups of plants as can be seen in **chapters 6 to 8**, although many still remain to be described. Within these works, I make mention of how the absence of these species from accessible areas, and from herbarium collections of the relatively well sampled Cordillera Urubamba, implies that these species are likely to be sensitive to human-induced grazing or burning and can only survive in areas with little disturbance. In **chapter 6**, I describe *Poa urubambensis*, a common species found in pristine forests of the Cordillera Urubamba, whilst also providing an up-to-date checklist and two keys for the open-panicled *Poa* species of Peru. During revision of herbarium specimens of Peruvian *Poa* specimens with open-panicled inflorescences, a further two undescribed species were also encountered and consequently described and a number of species names were placed in synonymy. In **chapter 7**, I describe *Bartsia lydiae*, another common species found in pristine forests of the Cordillera Urubamba, whilst also providing a key to *Bartsia* sect. *Laxae*, to which it belongs. In **chapter 8**, I describe *Moranopteris inaccessa*, a rare species found from inaccessible pristine forest-grassland matrix at the Abra Malaga site studied in chapter 1. This species also gains the elevational World record for species of *Moranopteris*, being found over 500 m higher than any other members of the genus.

Although undescribed species occupied a relatively small proportion and cover of accessible disturbed vegetation (see chapter 3), there were a few notable discoveries. In **chapter 9**, we describe the new species *Gentianella viridiflora*, found in the grazed edges of *Polylepis* forest at a site deep in the terrorist controlled region of the Cordillera Vilcabamba. These dangers, combined with the remoteness of the site, is probably why the species has not been collected until now, despite it being common at the type locality. Green flowered *Gentianella*'s are relatively uncommon, with it being suspected that this species is cleistogamous.

Whilst conducting the painstakingly detailed plant surveys of heavily grazed areas in the Cordillera Urubamba for chapters 2 and 3, a small plant was found in the plots that was so minute it could easily be confused with a moss on just a glance and formed the centrepiece in **chapter 10**. On closer inspection, we discovered this to be an angiosperm that had a Lobelioid-like resemblance but was much smaller than any currently described member and could, most probably, be the World's smallest dicot. Thus, with detailed molecular phylogenetic and taxonomic work, we determined this miniscule species as the smallest member of the Campanulaceae family, *Lysipomia mitsii*.

The great underlying theme of this project has been 'discovery', with discoveries in all shapes and forms permeating through every aspect of the project. There have been a number of newly established World records including the tallest high elevation forests [Chapter 4], the highest vascular epiphytes [Chapter 5], and the smallest Campanulaceae,

which is also probably the World's smallest dicotyledonous plant [Chapter 10]. The pristine ecosystems discovered consisted of unknown vegetation types dominated by new species to science [Chapters 1, 2 and 3] with a total of 17 undescribed species being discovered during the project [Chapters 1-3, 6-10]. From reconstructing the potential natural vegetation and soils of the high Andes, the discoveries can also be seen at a more important, but subtle, level as the research concludes that mankind has had a fundamental impact on the ecosystems of the high Andes and that human perceptions of what is natural need to be reevaluated with it being impossible to predict the properties of natural ecosystems in the absence of baseline data. This baseline data will have far reaching implications for our understanding of human influence on ecosystems and previous and potential biodiversity distributions, and will influence a wide range of fields ranging from paleoecology to conservation management and physiological ecology. I hope this thesis becomes the catalyst for a new wave of research using ecologically sound baselines to address key issues in ecological research, and I intend to continue pushing research in this direction.

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Most sites required at least a two or three day trek to arrive, with all our equipment being carried by horses or mules. The strong sun at these elevations meant that we invested in orange tarps to protect our tents from being burnt to a crisp during the prolonged time spent camping.

Once they get to know you, the local people are very hospitable, although many remained convinced that we were prospecting for gold. The women were remarkably shy and I think I must have caused quite a stir by flashing the occasional elderly village lady when washing in the mountain streams.

Basecamp at 4300 m.a.s.l. overlooking the prominent tower known by locals as 'Contorkayqu' or 'Where the condor nests'. Four expeditions were made to this site with a cumulative total of 2 ½ months being spent here sampling vegetation and soils.

Basecamp in the Phacchaq valley. A broken stove meant we constructed a makeshift 'cook house' to shelter the fire from the interminable rain and cook our meals during the month's stay here. Local helpers deserted us after one week due to the inhospitable conditions.

The climbing was often on loose, friable, vegetated rock, but we were the first ascensionists of a few nice routes, both during the fieldwork and during our free time, and we managed to free climb everything without the need for pitons, bolting or aid climbing.

Chapter 1

Inaccessible ledges as refuges for the natural vegetation of the high Andes

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Inaccessible ledges as refuges for the natural vegetation of the high Andes

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Keywords
Andes; Anthropogenic impact; Grazing impact; Peru; Polylepis; Potential Natural Vegetation (PNV) concept; Puna; Vascular plants

Abbreviation
PNV = Potential Natural Vegetation.

Nomenclature
W3TROPICOS (Solomon 1999)

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Abstract

Questions: Have millennia of human land use fundamentally altered the vegetation of a large proportion of the high Andean puna biome, with natural vegetation now restricted to inaccessible areas? Can inaccessible ledges be used as surrogates to infer the potential natural vegetation (PNV) in heavily impacted areas of the puna ecosystem of the high Andes? Is there a difference in plant community composition and diversity between the potential natural puna vegetation, represented by areas inaccessible to grazing and burning, and the anthropogenically disturbed vegetation found on nearby, but accessible, slopes?

Location: Abra Málaga Private Conservation Area, Cusco, southern Peruvian Andes.

Methods: Four study habitats were chosen that comprised ledges and slopes from within and outside of the conservation area. For each habitat, vegetation composition was recorded using eight to twelve 2 × 2-m^2 plots studied for species cover and abiotic variables.

Results: Analysis of species richness using two-way ANOVAs with Tukey test found that plots from the three habitats inaccessible to anthropogenic disturbance exhibited similar richness levels, whereas plots accessible to grazing and anthropogenic burning had significantly higher species richness. Likewise, CCA separated out plots of the three habitats inaccessible to anthropogenic disturbance from the unconserved slope plots. Species indicator analyses found the three inaccessible habitats to share the largest number of indicator species, with none being shared by the accessible, unconserved slope habitat. The PNV, inferred from the inaccessible vegetation, comprises a mosaic of *Polylepis pepei* woodland and tussock grassland, dominated by *Festuca* aff. *procera*, *Luzula gigantea*, *Valeriana mandoniana* and *Carex pichinchensis*.

Conclusions: As both the conserved and unconserved ledge habitats contain a vegetation that approaches that of the conserved slope, ledges can be taken as a surrogate to infer the PNV in heavily impacted areas where no conserved slopes are available. From preliminary data, the presumed PNV of the study area corresponds to a distinct vegetation assemblage including species previously unknown to science. Adjacent disturbed, accessible land contained a higher species diversity, with a flora that may have originated from localized, disturbed natural habitats.

Introduction

There is increasing evidence that the extensive high-elevation grassland biomes of the central Andes, known as the puna (when dry) or páramo (when humid), have been subject to intensive human land use for millennia, yielding a vegetation very different to what would naturally occur (Thompson et al. 1988; Burger 1992; Burns 1994; Chepstow-Lusty et al. 1996; Chepstow-Lusty & Winfield 2000; Moraes et al. 2006; Kuentz et al. 2011). Recent studies of the Cusco region of southern Peru, the epicentre for Incan societal development, have shown that pre-Incan civilizations, which date back more than 10 000 yrs BP, had already encroached on the highest Andean landscapes and

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developed agricultural practices to support the growing populations of humans and their associated camelid grazers (llamas and alpacas) (Burger 1992; Burns 1994; Chepstow-Lusty et al. 2009; Kuentz et al. 2011; Mosblech et al. 2012). Cutting of woodland for fuel and timber, grassland burning, livestock grazing and the creation of major terracing and irrigation systems all resulted in landscapes where natural vegetation was only preserved in the most inaccessible sites. This widespread anthropogenic impact has made it difficult to deduce what the natural vegetation should be in the high Andes.

Ellenberg (1958) was the first to suggest that the current patchy distribution of *Polylepis* (Rosaceae) woodland, now found as small relict stands in difficult to access areas, was due to poor human resource management, with burning, livestock grazing and timber extraction leading to its drastic decline. Further studies (e.g. Hensen 1995; Kessler 1995, 2000, 2002; Fjeldså 2002; Kessler & Schmidt-Lebuhn 2006; Renison et al. 2006; Cierjacks et al. 2007; Navarro et al. 2010; Hensen et al. 2012) have found evidence that *Polylepis* forests are an important component of the natural vegetation on mountain slopes throughout the Andes of Ecuador, Bolivia, Peru and northern Argentina. Pollen record studies by Hansen et al. (1984, 1994) from Junin, Peru, suggest that the major decline of *Polylepis* forest took place about 10 000 yrs ago, but it is still unclear whether this loss was mostly a consequence of climate changes, human activity, or a combination of the two.

Indeed, various authors have proposed that the current vegetation of the tropical Andes may be relatively close to the natural one, with *Polylepis* woodlands restricted to specialized microsites with deep soils and sheltered microclimate. This view is based on (1) vegetation studies showing a high diversity of regionally endemic plants in grazed vegetation types (e.g. Koepcke 1961; Simpson 1986; Rauh 1988); (2) topographic relationships shown by forest patches (Bader & Ruitgen 2008); and (3) palynological studies failing to show drastic declines of *Polylepis* woodlands in the last 5000 yrs and discounting previous declines as too early to have been caused by humans (van der Hammen & Hooghiemstra 2003; Paduano et al. 2003; Gosling et al. 2009). The original state of the natural vegetation of the tropical high Andes, thus, remains debated (Sarmiento 2000; Valencia et al. 2013).

A few studies have focused on the effects of burning and grazing on the more humid high-altitude páramo grasslands of Ecuador and Colombia (Williamson et al. 1986; Laegaard 1992; Hofstede et al. 1995; Keating 2000; Cárdenas-Arévalo & Vargas-Ríos 2008; Cierjacks et al. 2008; Valencia et al. 2013; White 2013), but available literature on the effects of grazing/burning on the drier puna landscape of Peru is limited (Wilcox et al. 1987; Becerra 2006), with only Seibert & Menhofer (1992) attempting to deduce what the potential natural vegetation should be. That study was based on the authors' opinion, with no objective data set being used, and highlights the central problem of the lack of baseline data available on what puna vegetation would actually look like should there be no human influence.

Thus, there is an urgent need to provide baseline data so that the natural vegetation and anthropogenically affected environments can be analysed objectively. The basic premise of the present study is that remote mountain ledges, which are only accessible with mountaineering equipment, harbour relict patches of near-natural vegetation that can be used as a baseline to deduce the natural puna vegetation, and hence provide information on both past human impact and the potential for ecosystem restoration. The study focuses on a private conservation area in the central Peruvian Andes where an enclosure experiment has been in place since 2001. This offers a unique opportunity to compare vegetation on both the slopes and inaccessible ledges within and outside of the fenced-off conservation area to assess if ledges can be used to deduce the potential natural vegetation of this puna grassland.

The main hypotheses addressed through the study are as follows:

1. Millennia of human land use (burning, grazing) have fundamentally altered the vegetation of a large proportion of the high Andes, including the Abra Málaga study area.
2. Examples of natural puna vegetation are nowadays restricted to sites such as crag ledges that are inaccessible without mountaineering equipment.
3. There is a difference in plant diversity and vegetation composition between the potential natural puna vegetation, represented by the areas inaccessible to grazing and burning (i.e. inaccessible ledges and accessible slopes of the fenced-off conservation area and the inaccessible ledges outside of the fenced-off conservation area), and the burned/grazed puna vegetation found on nearby, but accessible, slopes.

The aim of the present project is to validate the use of inaccessible ledges as indicators of natural vegetation so as to provide support for future research aimed at reconstructing the potential natural vegetation in areas where no grazing exclusion experiments or conservation areas are available.

Methods

Study area

The study was conducted within and around the Abra Málaga Private Conservation Area, Cusco, in the southern Peruvian Andes (13°08′S, 72°18′W, 4260–4490 m a.s.l.). The research area is at a confluence between the humid Cordillera Vilcabamba, with updrafts of humid air from the

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Amazon basin, and the dry Cordillera Urubamba. The climate is humid to semi-arid, with a clear wet season from November to April. Air relative humidity and temperature were recorded *in situ* using digital dataloggers (DS1923 Hygrochron iButtons; Hubbart et al. 2005), with one datalogger being placed at each site. Averaging these four data sources, mean daily air temperature of the study area was 4.3°C, with mean daily maximum temperatures of 9.4°C and mean daily minimum temperatures of 1.5°C. An absolute maximum temperature of 22.6°C was reached in November and an absolute minimum temperature of −22.0°C was also reached in the same month. Diurnal temperature fluctuations were very pronounced, especially in the dry season, with a mean daily temperature variation of 7.9°C and an absolute maximum variation of 36.0°C in November. Mean daily air relative humidity was 92.2%, with a mean daily minimum relative humidity of 76.5% and an absolute minimum of 13% reached in August. The vegetation of the site contained elements of flora characteristic of both the humid páramo, found in northern Peru (Marcelo-Peña et al. 2006; Tovar et al. 2011), and the dry puna, which occupies the majority of the high-elevation landscapes of central and southern Peru (Wilcox et al. 1986, 1987; Gutte 1987; Florez-Martínez 2005).

The Abra Málaga Private Conservation Area is the only stand of conserved *Polylepis* woodland in the Cusco region and has been fenced-off to livestock and had intentional burning of grassland and firewood harvesting prohibited since 2001 (Ecoan-Peru 2010). The fenced-off conservation area occupies 70.64 ha and is surrounded by heavily grazed puna grassland, with sheep, alpaca and llama corrals close by. The vegetation outside of the conservation area is subject to annual or biennial burning to remove undesirable tree saplings and old unpalatable tussock grasses, and to promote the resprouting of palatable new shoots. The conservation area is home to several threatened bird species, e.g. the Royal Cinclodes (*Cinclodes aricomae*), a *Polylepis* specialist and among the most threatened bird species worldwide, with an estimated population of 250 (Purcell et al. 2004).

Sampling design

The study area was partitioned into four sites (Fig. 1):

1. Conserved ledge (inaccessible ledges of the fenced-off conservation area).
2. Conserved slope (accessible slopes of the fenced-off conservation area).
3. Unconserved ledge (inaccessible ledges of the grazed/burned grassland surrounding the conservation area).
4. Unconserved slope (accessible slopes of the grazed/burned grassland surrounding the conservation area).

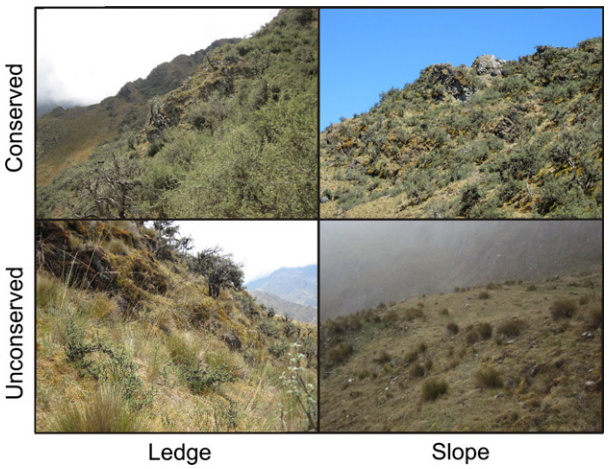

Fig. 1. Examples of the vegetation from the four sites studied. Sites with no human disturbance, i.e. the Conserved Ledges and Slopes, and Unconserved Ledges, all contained a mosaic of *Polylepis pepei* woodland intermixed with tussock grassland. The only site with anthropogenic disturbance, i.e. the Unconserved Slope, was characterized by a high diversity of plant species adapted to heavy grazing and annual to biennial burning.

All sites and plots were selected based on having a similar exposure, elevation, microclimate and inclination, with these abiotic variables being controlled for as much as possible among the sites so that differences in vegetation could be attributed largely to the level of accessibility to anthropogenic disturbance. Ledge sites were selected based on their degree of inaccessibility and presence of zonal vegetation and differed from slope sites in being surrounded by cliffs that inhibited access to grazing animals and the spread of human-induced ground fires from the surrounding landscape. These sites were accessed using mountaineering equipment. Distance between sites was kept to a minimum where possible, with the conserved sites being found about 1 km east of the unconserved sites. Slope sites, chosen for their deemed accessibility, were selected as close as possible to respective ledge sites, with a separation distance of 50–500 m. Ledge sites were comparable in most ecological conditions, especially the degree of soil and vegetation development, to slope sites, and did not represent azonal vegetation, i.e. pure rocky area. This judgement was based on ledge sites having deep soils (>50 cm topsoil) with a lack of soil mass movement at all sites.

Within each site, eight to twelve plots of 2 × 2-m^2 each were studied for species composition and abiotic variables from representative patches of vegetation. Plots were spaced with at least 5-m distance between them, and a maximum distance of 300 m from the nearest plot, to sample as much variability in the vegetation as possible. Voucher specimens were collected and identified in the field or

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in the herbarium and are deposited at CUZ, Z and LPB. Environmental variables studied include elevation, soil depth, stoniness of soil, wind exposure, slope inclination and aspect, air temperature, air relative humidity and percentage grazing of plots. Soil depth was measured in different parts of each plot using a metal rod driven into the ground until detained by the first rock and then measured. Stoniness of the soil was semi-quantitatively measured based on the soil depth measurements and given a categorical value of 0–100. Wind exposure was given a categorical value based on the author's opinion of the relative exposure of each plot to wind. Slope inclination was measured using a clinometer, with slope exposition being recorded using a compass. Air relative humidity and temperature were recorded at each of the sites using four digital dataloggers (DS1923 Hygrochron iButtons; Hubbart et al. 2005). Dataloggers were placed on raised platforms 10 cm from the soil surface and were sheltered from direct insolation. They were set to record at 2-h intervals over a 12-mo period from Oct 2010 to Nov 2011. Annual mean, daily mean minimum and maximum, and absolute minimum and maximum air temperatures and relative humidity were calculated from the data collected. The percentage grazing of each plot was recorded by overlaying a grid on the quadrat and estimating the vegetation cover that had been grazed.

Data analyses

We compared differences in species richness of the four study sites via two-way ANOVA with Tukey test. To compare species composition of plots across the study sites, canonical correspondence analysis (CCA; Ter Braak 1986) was performed on the data set with down-weighting of rare taxa. Detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS) were also applied but, since they gave qualitatively identical results, only the CCA results are shown here. To see which environmental vectors were significant in explaining the species composition of plots, abiotic variables recorded for each 2 × 2-m^2 quadrat were plotted on to the CCA. Finally, to identify the species characteristic of each site, indicator species analyses were performed using the Indval method (Dufrêne & Legendre 1997). Three separate Indval analyses were performed to compare and contrast the habitat types (1) Inaccessible (i.e. Unconserved Ledge, Conserved Ledge & Conserved Slope) vs Accessible (i.e. Unconserved Slope), (2) Conserved (i.e. Conserved Ledge & Conserved Slope) vs Unconserved (i.e. Unconserved Ledge & Unconserved Slope), and (3) Ledges (i.e. Unconserved Ledge & Conserved Ledge) vs Slopes (i.e. Unconserved Slope & Conserved Slope). The analyses were performed in R 2.15.2 (R Foundation for Statistical Computing, Vienna, AT) using the package 'vegan' v 2.0-5 and package 'labdsv' v 1.5-0.

Results

Vegetation survey and analysis

We recorded 58 species of vascular plant from the study area: 53 herbs, three sub-shrubs, one shrub and one tree (for species list, see Appendix S1). Twenty species occurred only in the grazed and burned Unconserved Slope site. The other three sites, which were free from grazing and burning, had more variable vegetation among plots within and between each site, with 19 species being found unique to these sites. Only two species were shared by all sites. One species of *Valeriana* and one species of *Moranopteris* (M. Sundue & M. Kessler, *unpubl. data*) are considered as undescribed and new to science, accounting for 3.4% of the total species richness of the study area.

Comparison of species richness between plots of the four sites, using two-way ANOVA with Tukey test, showed that the three sites inaccessible to grazing and burning contained similar levels of species richness per plot (Fig. 2). Plant diversity was generally low in these sites, with an average of 8.7 species per 2 × 2-m^2 plot. The Unconserved Slope plots, the only plots that were grazed and burned annually, differed significantly from the plots of the inaccessible sites by having a higher species richness, with an average of 16.3 species per 2 × 2-m^2 plot (Fig. 2).

In the CCA, axes 1 and 2 accounted for 11.2% and 8.3% of the total variance, respectively (Fig. 3). The plots of the three inaccessible, undisturbed sites clustered on

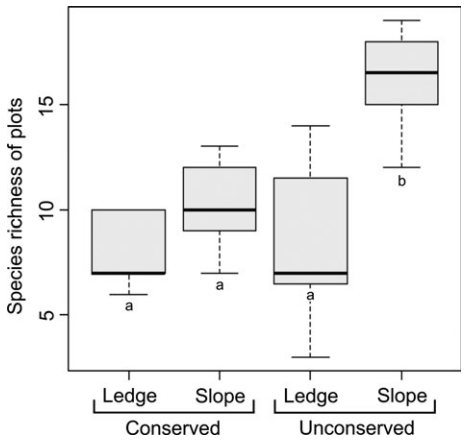

Fig. 2. Species richness per 2 × 2-m^2 plot in Conserved and Unconserved Ledges and Slopes. Large differences can be seen between the Unconserved Slope and the rest of the sites (two-way ANOVA, $F = 17.44$, $P < 0.001$; different letters denote significant differences following *post-hoc* Tukey test).

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the positive side of axis 1 and showed a clear separation from the accessible grazed/burned Unconserved Slope plots. When plotting environmental variables, the most strongly significant ($P < 0.001$) was percentage grazing of plots, which separated the Unconserved Slope plots from all other plots. Stoniness of the soil ($P < 0.01$) and wind exposure ($P < 0.05$) were also significantly associated with the Unconserved Slope, as this site experienced higher levels of erosion from livestock trampling and there was a higher degree of wind exposure due to the lack of shrubs and trees acting as windbreaks. Following this, the variables maximum soil depth ($P < 0.05$) and slope inclination $P < 0.01$) were also significant and separated the Conserved Slope plots from the other plots, as this site had much deeper soils and flatter topography compared with the other sites. The environmental variables related to air temperature and relative humidity were not significant in the analysis; neither were elevation and slope aspect.

Plant community composition

The indicator species analyses highlighted the differences in key species that characterized each of the four sites studied. Overall, 38 species had significant Indval values in at least one of the three analyses (App. S1), and can be considered as indicator species for the habitat types analysed. The largest and most significant differences in the number of indicator species were found between the inaccessible (i.e. Unconserved Ledge, Conserved Ledge & Conserved Slope) and accessible vegetation (i.e. Unconserved Slope; Fig. 4, App. S1). The undisturbed inaccessible vegetation, considered to be the potential natural vegetation of the study area, was comprised of a mosaic of *Polylepis pepei* woodland inter-mixed with tussock grassland dominated by *Festuca* aff. *procera*. Intermixed with the *Festuca* tussock grassland, other common species included *Luzula gigantea*, *Valeriana mandoniana* and *Carex pichinchensis*. Undescribed species of *Valeriana* and *Moranopteris* were also found exclusively in the inaccessible sites, accounting for 5.3% of the species richness from these sites, but were not significant in the indicator species analysis, possibly due to their low frequency. The accessible vegetation (i.e. Unconserved Slope) was found to share the most indicator species with the other habitat types, containing 12 indicator species of the slope vegetation and six indicator species of the unconserved vegetation (Fig. 4).

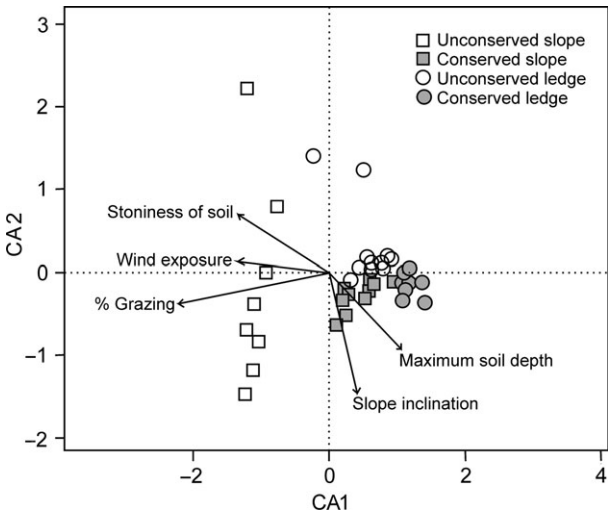

Fig. 3. Relative positions of the study plots along axes 1 and 2 from the CCA, showing the four sites studied. Arrows refer to the environmental vectors that were significant.

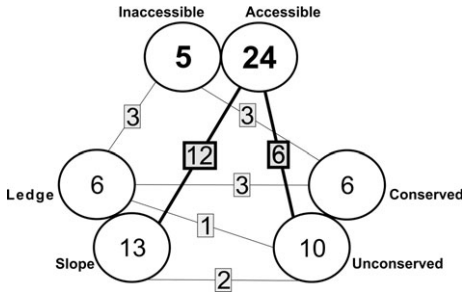

Fig. 4. Diagram to show distribution of the 38 species with significant ($P < 0.05$) indicator species (Indval) values after performing three separate analyses comparing the habitat types: (1) Inaccessible (i.e. Unconserved Ledge, Conserved Ledge & Conserved Slope) vs Accessible (i.e. Unconserved Slope), (2) Conserved (i.e. Conserved Ledge & Conserved Slope) vs Unconserved (i.e. Unconserved Ledge & Unconserved Slope), and (3) Ledges (i.e. Unconserved Ledge & Conserved Ledge) vs Slopes (i.e. Unconserved Slope & Conserved Slope). The paired circles represent the habitat types compared in the Indval analyses and the numbers within the circles refer to the number of indicator species representing that habitat type. The lines joining the circles and the numbers in boxes refer to the number of indicator species that were significant in both habitat types analysed. The largest differences in number of indicator species are in the accessible habitat type, which also shared the highest number of indicator species with other habitat types (Unconserved Slopes).

Discussion

The main hypotheses of the study were largely supported, with the three sites that are inaccessible to humans and livestock sharing roughly similar vegetation that can be considered as approximating the potential natural vegetation (PNV) of the study area. Furthermore, as the vegetation of the two ledge sites approximates that of the Conserved Slope site, this validates that the study of zonal vegetation on inaccessible ledges can be used to infer the PNV in heavily impacted areas of the puna, where conservation enclosures do not exist.

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There has been much debate regarding the PNV concept (Carrion & Fernandez 2009; Carrion 2010; Chiarucci et al. 2010; Farris et al. 2010; Loidi et al. 2010; Mucina 2010; Loidi & Fernandez-Gonzalez 2012; Somodi et al. 2012) and there are many different interpretations of PNV that can be adopted (Carrion 2010). In the present study, we adopted the concept that PNV is defined as 'a steady plant community which should be present in an area, as a consequence of the progressive succession, if there were no human influences. In practice, potential vegetation is considered synonymous to climax and to primitive vegetation (not altered yet by humans)' (Rivas-Martinez et al. 2002).

Unexpectedly, we found the PNV at Abra Málaga to comprise a distinct vegetation type that includes several plant species so far unknown to science. This vegetation type can be described as a mosaic of *Polylepis pepei* woodland inter-mixed with tussock grassland dominated by *Festuca* aff. *procera* along with other species such as *Luzula gigantea*, *Valeriana mandoniana*, *Carex pichinchensis* and rarer undescribed species of *Valeriana* and *Moranopteris*. None of these species were found in the accessible areas, presumably because they cannot tolerate the pressures of grazing and annual burning.

These interpretations of the PNV must still be taken with caution due to limitations inherent in the data set (Chiarucci et al. 2010). These limitations are based around the fact that PNV is a static concept and overlooks biological uncertainties, natural temporal variability, environmental heterogeneity and random neutral processes that form part of natural dynamic vegetation. Reconstructing PNV, in an ideal world, would require a study where demographic, ecophysiological and ecological factors are combined. Therefore, models of PNV that assume equilibrium of plant species with current climatic conditions are difficult to simulate and are prone to errors, especially in areas with a long-term human history (Baselga & Araujo 2010). As our experimental design only sampled a limited amount of the demographic, ecophysiological and ecological variability present within the Abra Málaga study area, we cannot conclusively say that the reconstructed PNV would occur in all parts of the study area.

Despite these uncertainties, the reconstructed PNV does support hypotheses that *Polylepis* forests are an important component of natural vegetation communities in the high Andes (Kessler 2002). Previous fossil pollen records and autecological studies (Hansen et al. 1984, 1994; Gosling et al. 2009) have claimed that the high Andes were once covered with a mosaic of *Polylepis* forest and puna grassland. The current patchy forest cover of *Polylepis* is estimated to occupy a mere 3% of its previous distribution in Peru (Fjeldså & Kessler 1996) with there being increasing evidence that modern human activity is having a detrimental effect on sustaining and re-establishing *Polylepis* forests (Renison et al. 2002, 2004, 2005; Teich et al. 2005; Cierjacks et al. 2007). In the Abra Málaga study area, timber and firewood extraction has resulted in the removal of almost all *Polylepis pepei* trees outside of the conservation area (ECOAN, pers. comm.), and intensive grazing and annual burning prevents the re-establishment of seedlings and saplings.

The Unconserved Slope was the only site subjected to high levels of anthropogenic disturbance and exhibited large differences in vegetation composition and species richness per plot compared to the other sites. There was much higher species richness per plot in this site as high levels of anthropogenic disturbance open up many niches so that no single species can become dominant and, instead, a multitude of herbs and forbs, including annual pioneer species, can become established. The flora encountered is widespread and common throughout the Andes of southern Peru (Mostacero-León & Mejía-Coico 1993; Pestalozzi-Schmid 1998; Mostacero-León et al. 2002a,b).

The species richness per plot of the PNV is much lower than that of the adjacent anthropogenically disturbed vegetation. This can be explained by how the low levels of disturbance result in a few species becoming dominant and out-competing other species. Interestingly, areas of natural disturbance (landslides, natural grazing by wild animals, etc.) within the potential natural vegetation did harbour species that are common to dominant in the grazed areas (e.g. *Poa perligulata*, *Carex ecuadorica*; S. Sylvester, *unpubl. data*), suggesting that these species occur in naturally disturbed microhabitats in anthropogenically undisturbed ecosystems (see also Kessler 1999, 2000). This is indirectly shown in the Indval analyses (Fig. 4, App. S1) by how the unconserved and slope habitat types contained high numbers of the indicator species that represent the accessible, grazed and burned vegetation.

Although all three inaccessible sites did exhibit similarities in vegetation, with the important indicator species corresponding to the PNV being prevalent, they were not identical and contained elements of the accessible Unconserved Slope vegetation (Fig. 4, App. S1). These differences in vegetation composition are most striking in the Conserved Slope site, which harbours a number of species associated with disturbance. Indeed, this was to be expected as the site has only had grazing, firewood extraction and burning prevented in the last 11 yrs. This relatively short time will not have been enough for succession to occur and allow the vegetation to reach equilibrium as a mature community. Despite this drawback of its relatively few years of establishment, the Abra Málaga conservation

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area is still the only fenced-off conservation area of this vegetation type in the Cusco region, and one of only a few others being implemented in the puna biome (Antamina 2010; Armonia 2013). Encouragingly, despite only 11 yrs of restrictions on anthropogenic disturbance, the vegetation is approximating that of the ledge sites.

Abiotic factors, despite all efforts to control for them, may also have had an influence on the vegetation composition of the sites and led to some of the differences observed. Maximum soil depth and slope inclination were the only environmental variables that were significant in separating out the three inaccessible sites, being positively correlated with the Conserved Slope plots (Fig. 3) and separated these from the two ledge sites, which had thinner soils and a steeper topography. Because the vegetation of the Conserved Slope, despite these differences in topography and soil depth, approximates that of the ledges, we argue that this indirectly provides stronger support for our reconstruction of the PNV as it shows that the same dominant indicator species can grow in a variety of different habitats. This refutes criticism that the reconstructed PNV may only coincide with areas having steep topography, like that of the ledge sites. Two plots from the Unconserved Ledge were also found to be floristically intermediate to the Unconserved Slope. The reasons for this, and the small differences between the two ledge sites, may be related to environmental factors that our experimental design failed to pick up (e.g. soil nutrient or cation content, microclimate, etc.).

The CCA analysis also implies that certain environmental vectors (i.e. wind exposure, soil depth, stoniness of the soil) were positively or negatively correlated with separating the accessible, Unconserved Slope plots from the other inaccessible plots. This could be seen as a criticism of the experimental design, in that we did not control for these abiotic variables sufficiently and so cannot truly infer the PNV. However, we argue that these vectors are indirectly affected by anthropogenic influence. Exposure to wind was significantly correlated with the Unconserved Slope site but this was due to a lack of trees and shrubs, which form natural windbreaks in the potential natural vegetation. Removal of woody trees and shrubs for firewood, as well as burning and grazing limiting re-establishment of seedlings and saplings, has thus resulted in a landscape that is more exposed. Soil depth was also negatively correlated with the Unconserved Slope vegetation, as high levels of disturbance by grazing animals have caused large-scale trampling and erosion so that soils are characteristically thin. This also explains why stoniness of the soil was significantly correlated with the grazed accessible site, as high levels of erosion from livestock trampling lead to soils that are thin and close to the bedrock, and thus have a higher stone content.

Conclusions

It has been suggested that most of the vegetation currently found in the high Andes has been modified by human activities, but this hypothesis remains untested because botanists, so far, have failed to survey potential undisturbed natural vegetation patches. The aim of the study has been to test whether zonal vegetation found on inaccessible ledges can be used as a surrogate to infer the PNV in heavily impacted areas of the puna ecosystem, where conservation areas or enclosure experiments do not exist. Indeed, we found that a distinct vegetation type, including plant species so far unknown to science, was present in the sites untouched by human disturbance, which presumably corresponds to the PNV of the study area. At the same time, besides differences in human impact, we were able to find zonal vegetation in all studied sites and thereby to control for environmental differences between them. Therefore, this study shows that inaccessible ledge habitats can be used to infer the PNV of the Andes even if protected areas are not available, as is the case almost everywhere. Naturally, the ledge sites chosen for such an exercise should be sufficiently large and flat to support zonal vegetation and not be strongly influenced by the rock faces sheltering them. The baseline data obtained from such studies will provide important insights into the natural ecosystems of the high Andes and, at the same time, benefit future conservation programmes in the Andes.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Table of Indval values for different species after performing three separate analyses comparing the site pairings: (1) Inaccessible vs Accessible, (2) Conserved vs Unconserved and (3) Ledges vs Slopes.

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Appendix S1. Supporting Information to the paper Sylvester, S.P., Sylvester, M.D.P.V. & Kessler, M. Inaccessible ledges as refuges for the natural vegetation of the high Andes. *Journal of Vegetation Science.* Indval values for different species after performing three separate analyses comparing the site pairings: 1) Inaccessible (i.e. Unconserved Ledge, Conserved Ledge & Conserved Slope) vs. Accessible (i.e. Unconserved Slope), 2) Conserved (i.e. Conserved Ledge & Conserved Slope) vs. Unconserved (i.e. Unconserved Ledge & Unconserved Slope), and 3) Ledges (i.e. Unconserved Ledge & Conserved Ledge) vs. Slopes (i.e. Unconserved Slope & Conserved Slope). The greatest differences are shown to be between inaccessible and accessible sites. Significant ($p < 0.05$) Indval values are in bold. Signif. codes: '***'=p<0.001, '**'=p<0.01,'*'=p<0.05, '.'=p<0.1.

Indicator species	Inaccessible	Accessible	Conserved	Unconserved	Ledge	Slope
Polylepis pepei B.B. Simpson	**1.00****		**0.70****		**0.67***	
Festuca aff. *procera* Kunth	**0.94****		**0.75****			0.11
Luzula gigantea Desv.	**0.81****		**0.87****		**0.57***	
Valeriana mandoniana (Wedd.) Höck	**0.69****		0.33		**0.60****	
Carex pichinchensis Kunth	**0.56***			0.27	0.32	
Senecio praeruptorum Sch.Bip.ex Klatt	0.42		**0.62****			0.34
Pernettya prostrata (Cav.) DC.	0.41		**0.41***			0.20
Valeriana sp. nov.	0.38		**0.40***		**0.38***	
Bomarea dulcis (Hook.) Beauverd	0.25		0.21		**0.30***	
Ranunculus krapfia DC. ex Deless.	0.22			**0.35****	**0.32****	
Lycopodium magellanicum (P.Beauv.) Sw.	0.14		0.28			**0.38****
Gynoxys nitida Muschl.	0.13		0.20		0.13	
Deyeuxia rigida Kunth	0.09			0.10	0.14	
Deyeuxia tarmensis (Pilg.) Sodiro	0.03			0.05	0.05	
Moranopteris sp. nov.	0.03			0.05	0.05	
Poa horridula Pilg.	0.03			0.05	0.05	
Werneria plantaginifolia Wedd. ex Klatt	0.03			0.05	0.05	
Cerastium glomeratum Thuill.	0.03		0.05		0.05	
Salpichroa glandulosa (Hook.) Miers.	0.03		0.05		0.05	
Agrostis perennans (Walter) Tuck.	0.03		0.05			0.06
Azorella multifida (Ruiz & Pav.) Pers.	0.03		0.05			0.06
Geranium sibbaldioides Benth.		**1.00****		**0.40****		**0.50****
Carex ecuadorica Kük.		**0.88****		0.26		**0.67****
Hypochaeris taraxacoides Ball		**0.88****		**0.35****		**0.39****
Poa perligulata Pilg.		**0.86****		0.33 .		**0.55****
Luzula racemosa Desv.		**0.82****		0.47		**0.78****
Lachemilla tanacetifolia Rothm.		**0.75****		0.21		**0.60****
Niphogeton dissecta (Benth.) J.F. Macbr.		**0.69****		**0.40****		0.26
Lysipomia sphagnophila Griseb. ex Wedd.		**0.63****		0.25 .		**0.28***

Indicator species	Inaccessible	Accessible	Conserved	Unconserved	Ledge	Slope
Azorella biloba (Schltdl.) Wedd.		**0.62****		**0.30***		0.27
Cerastium crassipes Bartl.		**0.60****		0.22		**0.44****
Gentiana sedifolia Kunth		**0.50****		0.20		**0.22***
Lysipomia laciniata A. DC.		**0.50****		0.20		**0.22***
Arcytophyllum filiforme (Ruiz & Pav.) Standl.		**0.45****		**0.25***		0.16
Deyeuxia recta Kunth		**0.42****		**0.25***		0.14
Belonanthus hispidus (Wedd.) Graebn.		**0.38****		0.15		0.17
Werneria caespitosa Wedd.		**0.38****		0.15		0.17
Oreomyrrhis andicola (Kunth) Endl. ex Hook. f.		**0.34***		0.11		**0.28***
Halenia caespitosa Gilg		**0.27***	0.06			**0.28***
Festuca asplundii E.B. Alexeev		**0.25***		0.10	0.44	
Distichia muscoides Nees & Meyen.		**0.25***		0.10		0.11
Huperzia crassa (Humb.&Bonpl.ex Willd.) Rothm.		**0.25***		0.10		0.11
Oritrophium limnophilum (Sch.Bip.) Cuatrec.		**0.25***		0.10		0.11
Plantago tubulosa Decne.		**0.25***		0.10		0.11
Uncinia macrolepis Decne.		**0.25***		0.10		0.11
Werneria villosa A. Gray		0.33		**0.49****		0.16
Agrostis tolucensis Kunth		0.31	0.21			0.19
Halenia weberbaueri C.K. Allen		0.31		**0.35***		0.10
Ourisia chamaedrifolia Benth.		0.18		**0.42***	0.19	
Jamesonia imbricata (Sw.) Hook. & Grev.		0.16	0.18		0.08	
Asteraceae sp.1		0.13		0.05		0.06
Bartsia peruviana Walp.		0.13		0.05		0.06
Lachemilla frigida (Wedd.) Rothm.		0.13		0.05		0.06
Oritrophium hieracioides (Wedd.) Cuatrec.		0.13		0.05		0.06
Plantago rigida Kunth		0.13		0.05		0.06
Senecio modestus Wedd.		0.13		0.05		0.06
Viola pygmaea Juss. ex Poir		0.13		0.05		0.06
Werneria nubigena Kunth		0.13		0.05		0.06

Chapter 2

Inaccessible Andean sites reveal human induced weathering in grazed soils

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Inaccessible Andean sites reveal human-induced weathering in grazed soils

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Abstract
Human activity affects properties and development of ecosystems across the globe, to such a degree that it is now challenging to get baseline values for undisturbed ecosystems. This is especially true for soil development, which is potentially affected by land-use history and holds a legacy of past human interventions. Therefore, it is still largely unknown for most ecozones how soil would have developed 'naturally'. Here, we show undisturbed soil development, i.e. the processes of weathering and accumulation of soil organic matter (SOM), by comparing pristine with grazed sites in the high Andes (4500 m) of southern Peru. We located study plots on a large ledge (0.2 km^2) that is only accessible with mountaineering equipment. Plots with pristine vegetation were compared to rangeland plots that were presumably under relatively constant grazing management for at least four millennia. Vegetation change, induced by grazing management, led to lower vegetation cover of the soil, thereby increasing soil surface temperatures and soil acidification. Both factors increased weathering in rangeland soils. Formation of pedogenic oxides with high surface area explained preservation of SOM, with positive feedback to acidification. Higher contents of pyrophosphate extractable Fe and Al oxides indicated the importance of organo-mineral associations for SOM stabilization on rangeland sites, which are likely responsible for a higher degree of humification. This higher degree of humification induced melanization (darker colour) of the rangeland soils which, together with sparse vegetation cover, also feeds back to soil temperature. With this work, we present a conceptual framework of positive feedback links between

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human-induced vegetation change, soil development and accumulation of SOM, which is only possible due to the unique baseline values of a pristine ecosystem. Using 'inaccessibility' as a tool to quantify human impact in future interdisciplinary studies may push research forward on evaluating anthropogenic impact on Earth's ecosystems.

Keywords
Anthropocene, feedbacks, grazing, human impact, mountain soils, soil development, soil organic matter, weathering

I Introduction

Anthropogenic alteration of ecosystems, landscapes and corresponding biogeochemical fluxes is spreading virtually everywhere across the globe (Rockström et al., 2009). Quantification of the human footprint has recently received great scientific and political interest (Malanson et al., 2014) with extensive global networks being set up to monitor changes in atmospheric trace gases, while land-use and land-cover changes are studied by more and more sophisticated remote sensing techniques. The human footprint has become so large that there is even debate over whether we have entered into a new geological epoch, called the Anthropocene (Crutzen, 2002). Although the term Anthropocene is now common in science, there is consensus neither on its existence nor on its start. There are arguments that the start of industrialization (c. 250 years BP; Crutzen, 2002), globalization (c. 60 years BP; Steffen et al., 2004) or anthropogenic alterations of soils (at least 2000 years BP; Certini and Scalenghe, 2011) should be used as a 'golden spike' to indicate the proposed start of this potential geological epoch. Certini and Scalenghe (2011) suggested the occurrence of Anthrosols ('man-made soil'; IUSS Working Group WRB, 2007) as the start of the Anthropocene.

According to Jenny (1941), soils are seen as the product of the cumulative influences of climate (cl), organisms (o), topography or relief (r), geology or parent material (p) and time (t), so the nature and properties of soil (S) is a function of these 'state-factors', expressed as:

$$S = \mathrm{f}(cl, o, r, p, t) \quad (1)$$

More recently, the state-factor model has been advanced to explain properties of whole ecosystems, and humans were included as a state-factor (Amundson and Jenny, 1997; Jenny, 1980). Although this is a widely accepted concept, the isolation of the influence of a single factor on soil genesis remains challenging. The reasons mainly are (a) autocorrelation, for example between climate and topography, and (b) unknown and temporarily varying land-use history (Amundson and Jenny, 1997). Climo-, chrono- or toposequences are used as tools for identifying the effects of these factors on soil formation (Amundson and Jenny, 1997; Chapin et al., 2012). An important challenge is to isolate human influence (Malanson et al., 2014). Anthropogenically induced changes may occur in high frequencies with different amplitudes and with time lags between events and effects on ecosystems and soil development (Richter, 2007). Direct quantification of anthropogenic effects on soil formation by experiments is nearly impossible to perform (Richter, 2007) and quantification by observation via paired plots is challenging (Leuschner et al., 2009), because it is necessary to find adjoining sites among which the only differing factor is the presence or absence of continuous, preferably static, human land-use.

Initial processes of soil formation are weathering of parent material and accumulation of

soil organic matter (SOM). Physical weathering essentially weakens or breaks structures of solid rock. Susceptibility to chemical weathering increases with increasing surface area and primary minerals are dissolved, transformed or translocated (Brimhall and Dietrich, 1987; Egli et al., 2003; Kleber et al., 2005; Schlesinger and Bernhardt, 2013). The weathering process of any material is strongly affected by temperature, moisture and proton activity (Amundson et al., 2007; Schlesinger and Bernhardt, 2013). Since land-use changes (1) are associated with vegetation changes, (2) can be associated with acidification (e.g. cation export by grazing or harvesting; Panichini et al., 2012), (3) alter the microclimate (energy budget, temperature, evapotranspiration, etc.; Foley et al., 2003) and (4) affect soil hydrological conditions (partitioning of infiltration, runoff and storage; Buytaert et al., 2006), it is likely that weathering processes in soil can be affected by human land management.

Chemical weathering is often quantified by chemical mass-balance approaches on pedon or watershed scales (Brimhall and Dietrich, 1987; Chadwick et al., 1990; Egli and Fitze, 2000; Price et al., 2012; White and Blum, 1995). Using a watershed-based approach, White and Blum (1995) analysed effects of climate on weathering rates of Si and Na from granitic parent material by comparing 89 sites. As expected, they could show that weathering rates increased with mean annual temperature and precipitation. Most importantly, White and Blum (1995) showed that temperature and precipitation had interactive effects: while weathering rates were linearly related to precipitation, the relation to temperature followed the Arrhenius equation (White and Blum, 1995). Consequently, increasing precipitation affects weathering rates more at high temperatures. This pattern was basically confirmed for alpine soils using pedon-scale mass balances. In most regions, however, gradients in climate are related to gradients in vegetation, which may interact with or superimpose effects of climate on soil development and weathering (Goudie and Viles, 2012; Verboom and Pate, 2013).

Plants affect weathering in basically three different ways: indirectly by (1) influencing water availability as well as directly by (2) altering solution chemistry and (3) distribution of elements across the soil profile (Goudie and Viles, 2012; Lucas, 2001). Water partitioning strongly depends on vegetation type. In general, forests exhibit higher evapotranspiration, compared to grass- and cropland (Foley et al., 2003). Therefore, under humid conditions downward percolation and, thus, leaching of weathering products is potentially higher in non-forest ecosystems. This effect was also shown by Price et al. (2012), where watersheds with lower forest cover had higher silica losses with stream water. Exudation of organic acids, as well as root respiration, changes the chemistry of soil solution. Acidic conditions enhance weathering speed. Moreover, organic substances in soil solution may form organometallic associations, theoretically enhancing or inhibiting mobility of metals and organic matter. By nutrient uptake and litter-fall, plants, especially trees, function as a 'biological pump' (Bockheim and Gennadiyev, 2000; Lucas, 2001). This process counteracts leaching of some elements ('biological base enrichment'; Bockheim and Gennadiyev, 2000) and also affects solution chemistry (Lucas, 2001). Whereas the general effect of plants on weathering (compared to the pure 'abiotic' process) is relatively well understood, the effect of vegetation types or functional species composition on weathering seems to be largely unknown (Verboom and Pate, 2013).

The same factors (temperature, precipitation, vegetation) affecting weathering are also involved in processes of SOM accumulation. Vegetation markedly affects the quantity and quality of organic matter input in soil, whereas acidification, temperature and moisture essentially affect decomposition processes (Jenny, 1941; Swift et al., 1979). Contrary to anthropogenically induced changes in weathering,

changes in the terrestrial carbon pool have received great interest in recent years, even though both are linked. Therefore, weathering should be included in concepts and models for soil carbon accumulation and sequestering (Amundson et al., 2007).

Estimates of terrestrial C-loss driven by land-use changes are in the range of 48–114 Pg until 1850 and then 108–188 Pg in the industrial era (Houghton, 2012), with about 25% of the loss originating from SOM. However, quantifying below-ground C stocks is tedious (Jungkunst et al., 2012) and this is even more true for quantifying their changes (Heitkamp et al., 2012). Basically, two challenges exist: (1) the lack of, or objective choice of, reliable baseline values and (2) the natural variability of soils (White and Walker, 1997). Extensive grazing management is one of the earliest and most widespread human activities. Globally, about 1.5 billion people depend on livestock and about 70% of agricultural land (25% of the ice-free Earth surface) is used as pasture or rangeland (Neely et al., 2009). Many pasture and rangeland soils are degraded, which is a threat to the livelihood of those dependent on livestock while also forming a source of atmospheric CO_2 (Conant, 2012; Neely et al., 2009). Smith et al. (2008) estimated that 2 Pg of atmospheric CO_2 could be sequestered per year in pasture soils until 2030 by improved management and restoration. Such estimates require data of best management practice, but, ideally, also baseline values for 'natural' conditions as reference values (White and Walker, 1997). However, a major shortcoming is the lack of pristine sites to quantify reference values. Hence, only decades of land-use change or land-use abandonment can be compared to continuously used land in experimental approaches, such as fencing. Most studies reviewed by Tanentzap and Coomes (2012) have durations of, at most, a few decades. Consequently, effects of grazing exclusion on SOC stocks were on average around zero in most ecosystems (between decreases of 1.5 to increases of 3.8 Mg C ha^{-1}) and only limited conclusions could be drawn regarding long-term (centuries or millennia) effects of soil degradation and recovery. Two major concerns arise from these experimental studies: (1) the timescale is hardly long enough to induce major effects on pedogenesis (Richter, 2007) and (2) the 'treatment' is recovery from management and the 'control' is used land and not the natural ecosystem state. Only one study claims a control site that was never grazed (Neff et al., 2005). This study was located in Utah, USA, and grazing management by cattle ranchers took place from 1900 to 1974. Results showed strong effects of wind erosion on grazed sites as well as depletion of SOM and soil microbial biomass. However, the grazing period was limited to some decades, and the former land-use by natives remains unknown. Besides environmental conditions, accumulation of SOM in soils is also strongly determined by organo-mineral interactions (Heitkamp et al., 2012; Schmidt et al., 2011). Pedogenic oxides and clay, which develop during weathering of parent material, provide a highly reactive surface area, and SOC is stabilized by various sorption mechanisms in the form of organo-mineral complexes. If weathering would be altered by human impact, this would, in turn, also have effects on SOC accumulation.

In this study, in the high Andes of southern Peru, the human state-factor is isolated by comparing adjoining sites which differ in their level of accessibility to grazing livestock and human-induced ground-spreading fires. These sites are identical in climate, time, parent material and topography, but differ in their land-use history by the inaccessibility of one of the two sites. The accessible site has been subject to constant grazing and burning of the vegetation most likely continuously over several millennia. Here we investigate if pristine and grazed sites, differing in the state-factor 'humans' by inaccessibility, reveal different trajectories in soil development, i.e. weathering and accumulation of organic matter.

II Land-use history of the region Cusco, Peru

Hunting activities in the Andes have been documented by bone deposits, dating back to the end of the last glacial period (Marin et al., 2007; Wing, 1974) but the early ecological impact of men remains uncertain (MacNeish, 1971). Domestication of camelids began some 6000 years ago (Wheeler, 1988; Wing, 1974) and quickly led to widespread soil erosion as documented by lake sediments (van der Hammen and Noldus, 1985) and dust deposits on Andean glaciers (Binford et al., 1997; Thompson et al., 1988). It has been hypothesized that the social and cultural development of Andean cultures was driven by the ecological degradation of Andean ecosystems and agrosilvopastoral innovations, especially as a result of periodic drought phases during which human population densities exceeded the carrying capacity of these ecosystems (Bauer, 2004; Chepstow-Lusty et al., 2009). During the Inca period (c. AD1000–1533), up to 20–30 million people are believed to have inhabited the central Andes (Bauer, 2004). Palynological evidence indicates that reforestation was actively promoted by the Incas in their effort to restore Andean ecosystems (Mosblech et al., 2012). When the Spaniards arrived in the Andes, they encountered a densely settled landscape with huge agricultural areas and camelid herds numbering in the tens of millions (Sanabria Fernandez et al., 1961). The human population crash of up to 80% after the conquest (Bauer, 2004; Crosby, 1986) appears to have led to some ecological recovery (Mosblech et al., 2012). The human footprint is not only restricted to regions close to large population centres but extends to even the most remote regions (Toivonen et al., 2011). Hunters and pastoralists can be found days away from the closest human settlements and commonly use fire to clear grasslands for hunting or as grazing grounds (Kessler, 2002). Accordingly, over

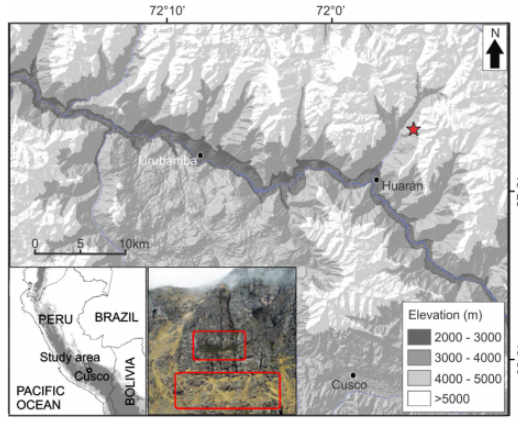

Figure 1. Digital elevation map of the study area. The star indicates the sampling location. The photo shows the pristine site in the centre and the rangeland site in the lower part of the picture.
Source: ASTER DEM raster map provided by METI and NASA Land Processes Distributed Active Archive Center.

99% of the Andean landscapes have been directly affected by human use, mostly extending over millennia, to such a degree that the natural condition of soil and vegetation is largely unknown. Up to 98% of the native high Andean forest vegetation has been removed and it is likely that the grassland vegetation that now dominates these landscapes is of anthropogenic origin (Kessler, 2002).

III Methods

1 Location and site conditions

The study site, locally called 'Cancha Cancha', is situated in the Cordillera Urubamba in Cusco province, southern Peru, 30 km north of the town of Urubamba (13°14′35″S 72° 1′18″W) at 4500 m a.s.l. (Figure 1). According to Troll (1968), the site is located in the puna belt within the 'tierra helada' which is characterized by low annual mean temperatures, a high diurnal temperature amplitude and a semi-humid climate with a pronounced dry season from May to

October. Mean annual precipitation in the closest climate stations ranges from 454 mm (Urubamba, 2863 m a.s.l.) to 1606 mm (Winaywayna, 2800 m a.s.l.) (Toivonen et al., 2011). Since our study site lies 1600 m above the climate stations, the data are hardly comparable. Nevertheless, orography and vegetation pattern in Cancha Cancha indicate that mean annual precipitation ranges at the higher end of these records. Air temperatures were recorded at the site using sensors and digital data loggers (DS1923 Hygrochroni Buttons). Since Cancha Cancha is less than half a day's travel away from the bottom of the Inca's fertile 'Sacred Valley', it is likely that the site has been intensively used as rangeland for, at least, 4000 years.

The pristine site was formed of zonal vegetation located on a ledge of approximately 0.2 km^2 size. Inaccessibility was guaranteed by steep mountain cliff faces (Figure 1) that inhibited access to grazing animals and the spread of human-induced ground fires from the surrounding landscape. The site could be accessed from above by a 60 m controlled descent down the cliff using mountaineering equipment. The accessible site plots were located as close as possible to the pristine site, with the distance no more than c. 500 m. Both sites were well above the shoulders of the U-shaped valley, indicating no direct glaciation in the last glacial maximum. The aspects of all plots were similar in NW direction and ranged from 290° to 310°. Animal trampling was widespread on accessible slopes, as typical for the whole region. An impression of the landscape and the different plots is shown in Figures 1 and 2.

2 Vegetation records

We partitioned the study area into two main habitats: (1) pristine forest/grassland mosaic located on the inaccessible cliff ledge mentioned above (Figure 2, a–f); and (2) rangeland (Figure 2, g–i), located on the accessible grazed slopes surrounding the pristine site, that was formed of mostly herbaceous taxa, some woody shrubs and single trees. The pristine forest/grassland mosaic consisted of different vegetation types, i.e. forest with a densely closed canopy, interspersed with several forest gaps dominated by bunchgrasses. No forest was found in accessible areas due to excessive timber and firewood extraction from the local campesino population of Cancha Cancha (Sylvester, personal observation).

Within each habitat, we studied 20–33 2 × 2m^2 plots for species composition and abiotic variables from representative patches of vegetation. Voucher specimens were collected and identified in the field or in the herbarium and are deposited at the herbaria of Cusco, Peru (CUZ), Zurich, Switzerland (Z), and La Paz, Bolivia (LPB). Abiotic variables studied include elevation, soil depth, slope gradient and aspect. Abiotic variables were controlled for as much as possible between habitats with quadrats being placed in areas with similar aspect, elevation, etc., so that differences in vegetation could be attributed largely to the level of accessibility.

3 Sampling and soil characterization

In the field we chose three pits per vegetation type (pristine forest, pristine grass and rangeland). A different slope angle class was chosen for every replicate within each vegetation type. According to the guidelines of soil description (FAO, 2006), slope classes were strongly sloping (10–15%), moderately steep (15–30%) and steep (30–40%). No obvious signs of erosion were visible. Due to the thickness of the A-horizon, sampling was done in strata (0–5, 5–10, 10–20, 20–30, 30–40 cm). For every depth increment, we took a known volume of sample from the profile wall by the volume replacement method described in Maynard and Curran (2008). We combined triplicate samples to one bulk sample of 300–500 ml volume.

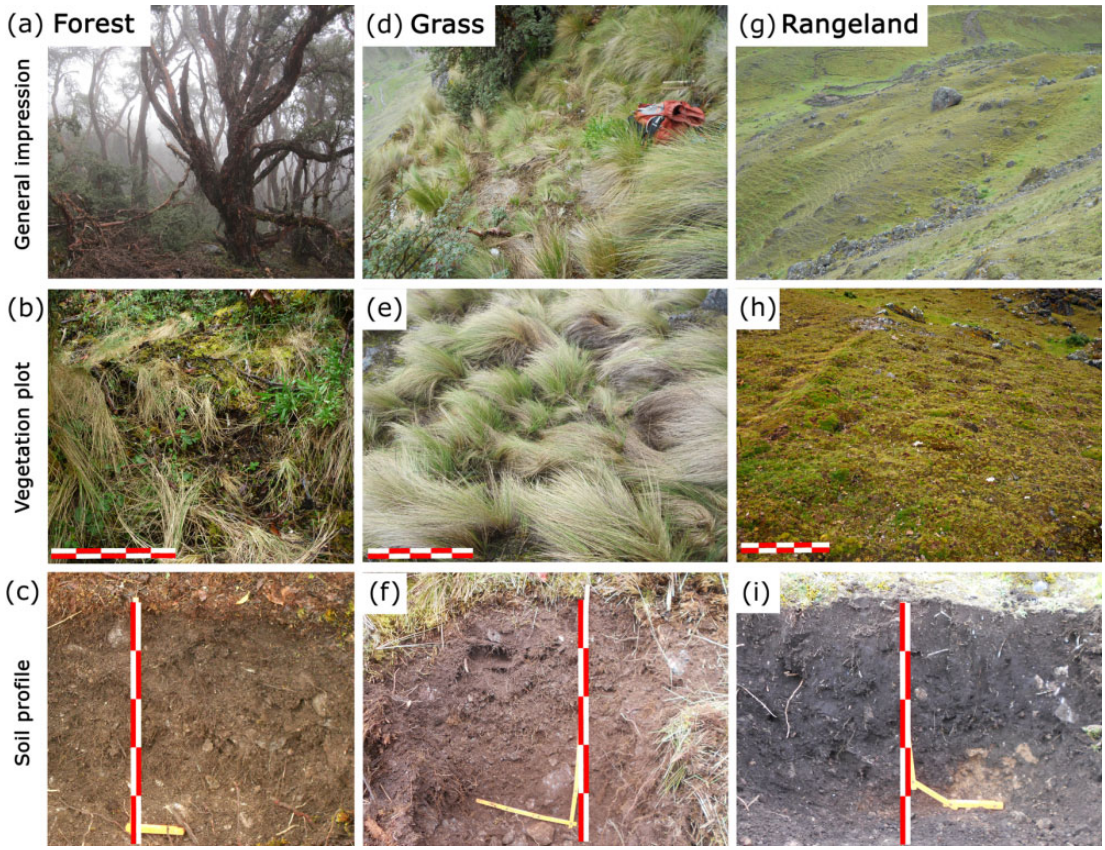

Figure 2. Photos showing the general impression (upper row), the vegetation plots (middle) and the soil profiles (lower row) for the forest (a, b, c), grass (d, e, f) and rangeland (g, h, i) ecosystems. The inserted scales are 50 cm with 10 cm increments. In the vegetation plots, the scale is approximate and only valid in the foreground of the photo.

Mean values of the profiles (n = 3) were used for presentation of data. Determination of soil types followed strictly the revised version of the world reference base (IUSS Working Group WRB, 2007), including properties quantified in the laboratory analysis.

4 Laboratory analysis

Field moist samples were weighed and subsequently sieved (2 mm). We cleaned the residue on the sieve with tap water and sorted it into roots and rock fragments (>2 mm). We dried roots at 70°C and rocks at 105°C, and both were weighed after cooling in a desiccator. We dried a subsample of the fine earth at 105°C (48 hours) to determine moisture content, another subsample at 40°C for analysis, and the major part was stored moist at 4°C in the dark (van Reeuwijk, 2002). The following equations were used to calculate the mass of fine earth per square metre (Maynard and Curran, 2008):

$$\rho_{w,i} = \frac{W_{fe,i} + W_{r,i}}{V_i} \quad (2)$$

$$M_{w,i} = \rho_{w,i} \times h_i \quad (3)$$

$$M_{fe} = \sum_{i=1}^{n} \frac{M_{w,i} \times 100}{(W_{r,i}/W_{fe,i} \times 100) + 100} \quad (4)$$

where ρ_w is the bulk density of the weathered pedon (i.e. fine earth and rock fragments; g cm^{-3}) of layer i, $W_{fe,i}$ is the weight of oven-dry fine earth (g) of layer i, $W_{r,i}$ is the weight of rocks (g) in layer i, V_i is the total volume (g cm^{-3}) of the undisturbed sample (i.e. the hole in the profile wall) in layer i, $M_{w,i}$ is the mass of the weathered pedon (kg m^{-2}) in layer i, h_i is the height (mm) of layer i and M_{fe} is the mass of fine earth (kg m^{-2}) of the whole profile. The bulk density of fine earth (ρ_{fe}, g cm^{-3}) of layer i was calculated as:

$$\rho_{fe,i} = \frac{W_{fe,i}}{V_i - (W_{r,i}/2.65)} \quad (5)$$

where 2.65 is the assumed density of rocks (g cm^{-3}).

We determined particle size distribution by sieving and sedimentation (van Reeuwijk, 2002). Values of pH were determined in 0.1 M $CaCl_2$ solution in a 1:5 soil: solution (*v/v*) ratio (ISO, 2005). $CaCl_2$ was chosen, because Ca was dominant on the exchange sites. Effective cation exchange capacity was determined by extraction with 1M NH_4Cl (Lüer and Böhmer, 2000). We measured cations by ICP-OES (Optima 4300 DV, Perkin Elmer Instruments, Norwalk, USA). Total carbon and nitrogen contents were measured by dry combustion (950°C, Truspec CHN LECO, St Joseph, MI, USA). Due to the low pH, we assumed no presence of carbonates and total carbon thus equals SOC. Stocks of SOC were calculated as the product of concentration and mass of fine earth. We determined total element concentrations in soil and parent material after HNO_3/HF digestion (König and Fortmann, 1999) with ICP-OES. In the same extracts, rare earth elements (REE) were measured by ICP-MS (PlasmaQuad STE, Fisons/VG, Winsford, UK). REE concentrations were normalized to Cl-chondrite values (Anders and Grevesse, 1989) and presented as so-called Spider diagrams, i.e. the REE are arranged by their atomic weight on the x-axis against the logarithm of chondrite-normalized REE concentrations on the y-axis. These were often used in provenance studies of different materials due to their unique signatures (Kurtz et al., 2001; McLennan and Taylor, 1991). Therefore, Spider diagrams of REE are ideally suited to indicate homogeneity of bedrock and soil (Caspari et al., 2006), i.e. if bedrock is the unique parent material or not (Sako et al., 2009). Using total element concentrations, the chemical index of alteration (CIA;Nesbitt and Young, 1982) was calculated as a molar ratio (note that the molar ratio of oxides was used originally):

$$CIA = \frac{Al}{Al + Ca + Na + K} \times 100 \quad (6)$$

Fractions of Fe and Al were extracted with sodium dithionite-citrate-bicarbonate (Fe_d and Al_d), ammonium oxalate (Fe_o and Al_o) and sodium pyrophosphate (Fe_p and Al_p) and element concentrations were measured by ICP-OES as described in van Reeuvijk (2002). Oxides develop during pedogenesis due to weathering of parent material. In general, every agent is supposed to extract specific forms of Fe and Al. Extraction with sodium dithionite-citrate-bicarbonate is a measure for the sum of pedogenic Fe oxides and includes crystalline, amorphous and organically complexed forms of Fe. This extraction is less specific for forms of Al and Si. Extraction with ammonium oxalate is a measure for amorphous and organically complexed Fe and ammonium oxalate is supposed to extract imogolite, allophanes, poorly defined aluminosilicates and organically complexed forms of Al. Furthermore, ammonium oxalate extracts Si from allophanes. Extraction with sodium pyrophosphate is generally used to quantify organically complexed forms of Fe and Al. Several ratios can be calculated indicating different processes. The Fe_o/Fe_d ratio indicates the degree of crystallization of Fe oxides. In general (aerobic conditions), crystallization increases with time of soil development (Torrent et al., 1980), but can be affected by

Table 1. Vegetation characteristics end of March/beginning of April 2011.

	Pristine		Managed		
	Forest (n = 15)	Grass (n = 7)	Rangeland (n = 26)	CV_P	$p<F$
Bare soil (%)	4[a]	2[a]	21[b]	± 83%	<0.001
Litter cover (%)	60[a]	64[a]	4[b]	± 48%	<0.001
Forb height (cm)	24[a]	31[b]	3[c]	± 63%	<0.001
No. of forb species	8[a]	6[a]	28[b]	± 28%	<0.001
Canopy cover (%)	56	–	–	± 56%	–

CV_P: pooled coefficient of variation

vegetation or presence of certain organic substances (Dümig et al., 2008). The ratios of Fe_d/total Fe (Fe_T) and Al_o/total Al (Al_T) indicate the states of weathering and degree of soil development (Torrent et al., 1980; Vacca et al., 2009).

5 Statistics

Concentration data for the whole soil profile (A-horizon) were averaged by weighting according to soil mass in the corresponding layers. We checked the data for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levène test). In the few cases of skewed distributions the data was successfully log-transformed. All variances were homogeneous. We treated the data as a balanced and fully randomized design. We performed one way-ANOVA with SPSS (IBM SPSS Statistics 20.0.0), followed by Fisher's least significant difference in case of significant ($p \leq 0.05$) effects (Webster, 2007). We calculated the pooled coefficient of variation as a measure of dispersion.

IV Results and discussion

1 Vegetation

Pristine sites represented a mixture of *Polylepis subsericans* J.F. Macbr. forest of different closures and bunchgrass-dominated clearings. This forest mosaic is presumed to be the original vegetation in large parts of the region (Fjeldså, 2002; Kessler, 2002). The trees provide relatively dense crown cover (56%) and grow to an average height of almost 5 m (Table 1). There was little bare soil on the ground, which was covered by densely rooted litter consisting of exfoliated bark and some leaf litter. On average, eight species of bunch grasses and herbs were found in each 2 ×2-m square in the understorey. Six species were found in the bunch grass clearings, which were dominated by tall *Deyeuxia* spp. and *Festuca* spp. bunch grasses (Figure 2). The species richness per square area was significantly lower in these pristine grasslands than in the rangelands, presumably because the bunch grasses outcompeted smaller herbs (Borer et al., 2014). Bunch grasses are well known to be susceptible to fire and strong grazing pressure, and their scarcity in the rangelands is in accordance with previous studies in, for example, North America (Collins et al., 1998; Fuhlendorf and Engle, 2001).

Vegetation of the rangeland sites was very different (Figure 2, g and h). The mean vegetation height was only 3 cm at the end of the rainy season, when vegetation development was at its maximum. Litter was practically absent and the proportion of bare soil was much higher (21%) in comparison with the pristine sites (2–4%, Table 1). This result indicates the high grazing pressure on these rangelands, which are situated close to human settlement (30–60 minutes' walk). The higher species richness per square area in rangelands presumably reflects the influence of disturbance which inhibits the dominance of highly competitive species (Connell, 1979; Warren et al., 2007). For instance, grazing

prevents fast-growing and shade-tolerant species from outcompeting slow-growing and light-demanding plant species, thereby opening up niches for a higher number of different species (Borer et al., 2014). The continual burning and grazing on the rangeland sites favours the establishment of plants with adaptations to survive these anthropogenic pressures, such as the ability of species to grow close to the soil surface, the presence of toxins in their leaves, or spiny habit. These findings are in line with other studies conducted in the puna (Wilcox et al., 1986) and páramo (Lægaard, 1992).

Thus it appears that human land-use led to fundamental changes in the vegetation, from a dense, species-poor, tree- and bunch grass-dominated ecosystem with high above-ground biomass to an open, species-rich and herb-dominated system with very little biomass (Figure 2). While no temporal data are available, the longevity of the plants in the pristine ecosystems suggests that these are rather stable over time, whereas the herb-dominated vegetation in grazed sites may well be more dynamic. For example, a close-by, fenced-off area without grazing at Abra Málaga (c. 30 km northwest of this study's location) showed marked differences in the herb vegetation after only 11 years of fencing compared to nearby grazed sites (Sylvester et al., 2014).

2 Bedrock

The bedrock was classified as vulcanite Andesite, as also described by Mamani et al. (2010) for this region. It was characterized by high portions of fine-grained matrix with embedded plagioclase feldspar, quartz crystals and little chlorite. Some differences between the thin sections (Figure 3) from pristine and rangeland plots occurred: in the sections of the pristine site, more quartz-filled cracks occurred, the amount of matrix material was slightly higher and more veins and embedded particles of black, opaque material (ore) were present. However, bulk elemental composition was not significantly different between the samples (Table 2) and they had the same mineralogical assemblage. Moreover, only two thin sections were analysed, whereas chemical composition was measured for every profile.

Patterns of rare earth elements indicate that most profiles were derived from similar bedrock. Only profile 9 (Figure 4) showed deviation from the other REE pattern by not having a pronounced negative Europium (Eu) anomaly (i.e. lower concentrations of Eu compared to the neighbouring elements; McLennan and Taylor, 1991). This indicates different conditions in the original melt (i.e. plagioclase fractionation; McLennan and Taylor, 1991), which is also expressed in the chemistry of the rocks: the relatively high K content with a high coefficient of variation in rocks of rangeland plots (Table 2) was induced by the higher K concentration mainly in profile 9.

3 Homogeneity of parent material

Soils on slopes are potentially prone to erosion and mass movements. Hence, mountain soil profiles are often truncated or buried (sedimentation or rockfall). Furthermore, atmospheric inputs of dust or volcanic ashes may markedly contribute to parent material (Derry and Chadwick, 2007; Kurtz et al., 2001). With the aim of comparing pedogenesis with and without anthropogenic influence, it is essential to underpin the assumption of *in situ* development of the profile. There are indicators that the chosen profiles in this study were not buried, did not experience major amounts of rockfall and did not receive larger amounts of allochthonous dust or volcanic ash inputs:

- The content of rock fragments (Figure 5) gradually increased downward. This pattern is typical for *in situ* pedogenesis: the weathering front proceeds from the top downwards, so the topsoil is the part of

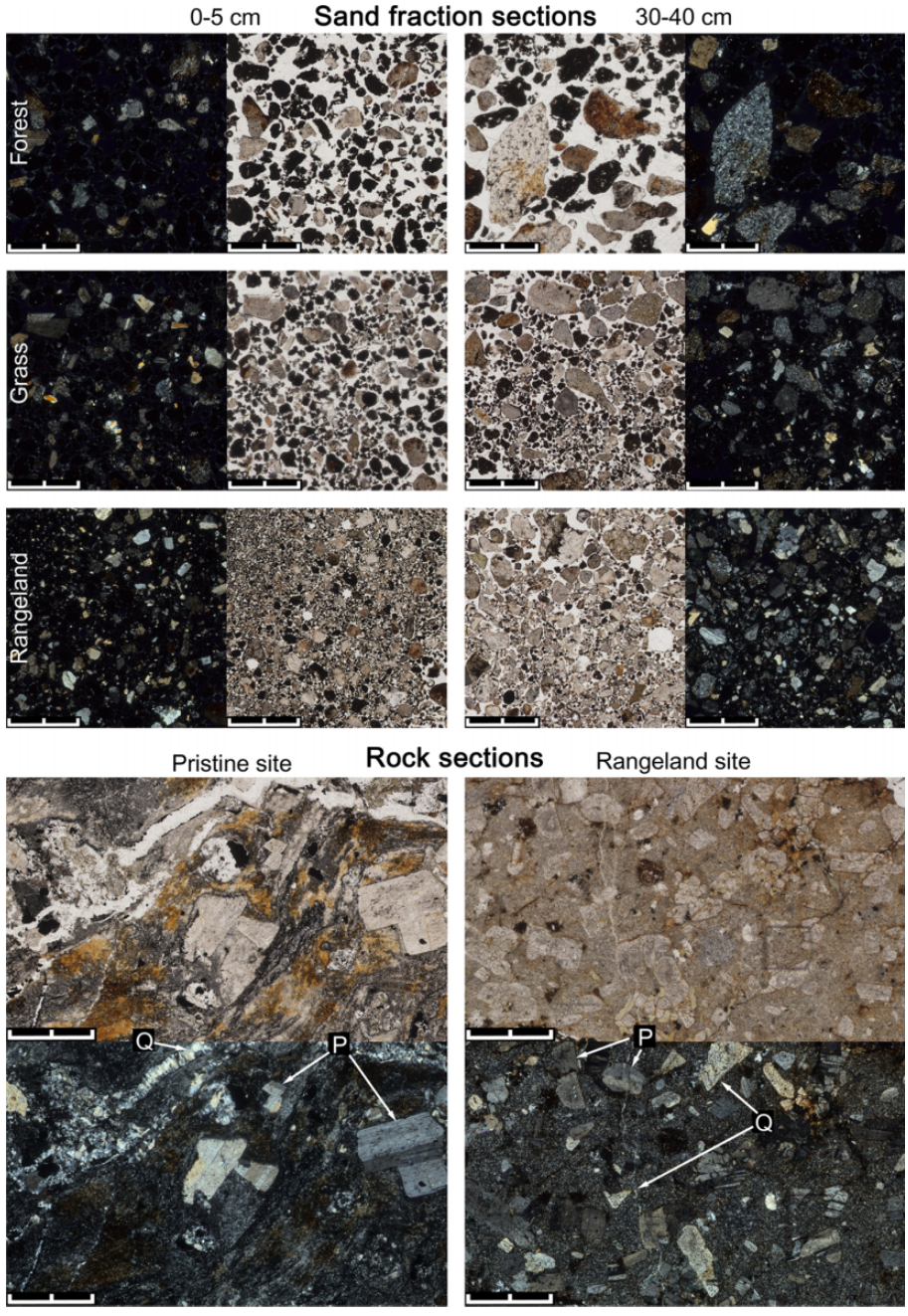

Figure 3. Thin sections of sand fractions (samples from 0–5 and 30–40 cm depth) and rocks. The scale bar is 2 mm in total. The dark pictures show the sections with crossed polarizers. Plagioclase (P) and quartz (Q) are indicated in the picture of the rock sections.

Table 2. Element concentrations of soil and parent material as weighted mean for the entire A-horizon (n = 3).

	Pristine		Managed		
	Forest	Grass	Rangeland	CV_P	$p<F$
Bedrock					
Al (g kg^{-1})	80.4	77.4	84.9	± 3%	0.086
Ca (g kg^{-1})	5.0	4.6	5.9	± 40%	0.743
Fe (g kg^{-1})	41.8	40.9	51.8	± 35%	0.703
K (g kg^{-1})	2.4	1.6	12.7	± 56%	0.556
Na (g kg^{-1})	45.4	43.7	36.2	± 20%	0.323
Soil					
Al (g kg^{-1})	57.1	60.2	71.8	± 13%	0.112
Ca (g kg^{-1})	6.4	3.2	2.2	± 48%	0.088
Fe (g kg^{-1})	30.9	34.9	42.6	± 29%	0.504
K (g kg^{-1})	7.0	7.6	10.8	± 36%	0.477
Na (g kg^{-1})	28.6	29.0	23.9	± 29%	0.640

CV_P: pooled coefficient of variation.

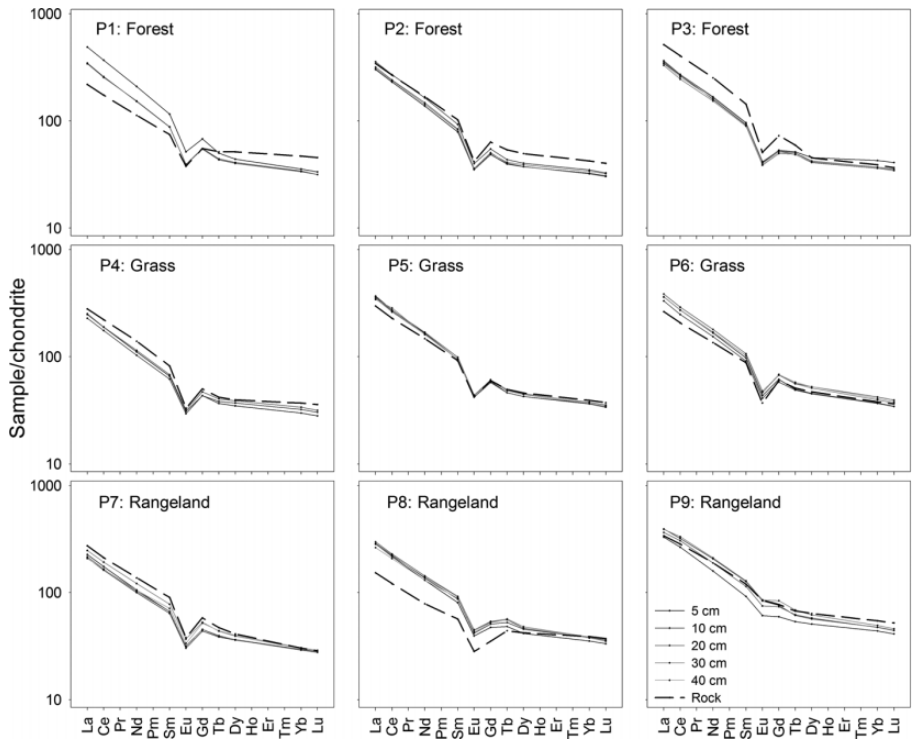

Figure 4. Spider diagrams of chondrite-normalized rare earth elements. The elements are arranged according to their atomic number on the x-axis, starting with the lowest (Lanthanum, 57) and finishing with the highest (Lutetium, 71).

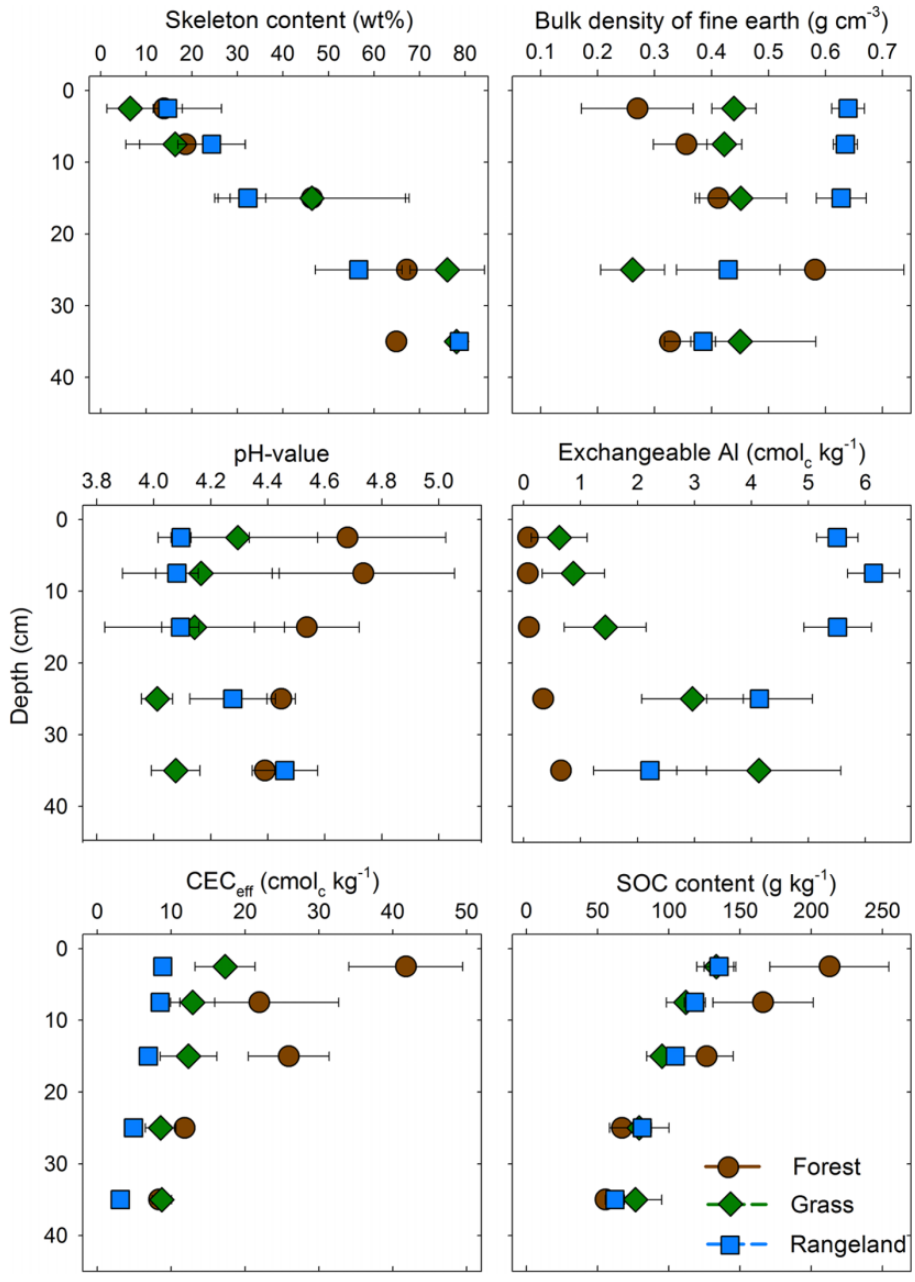

Figure 5. Soil properties of the A-horizons in different depth increments. Mean values of three profiles with standard errors, apart from pH-values where the range is given instead.

the profile with the longest weathering history (Jenny, 1941; Legros, 2013). Therefore, a higher proportion of parent material is transformed into soil, i.e. the amount of rock fragments increases with depth (Zech and Hintermaier-Erhardt, 2002). Differences between sites were not significant and standard errors increased

with depths. This pattern of coarse fragment distribution indicates that rockfall was not important during the time of pedogenesis. Otherwise, contents of coarse fragments would have been higher on top of the profile, or sudden shifts in rock content would have been observed.

- The morphology of the sand fractions were different between samples taken from 0–5 or 30–40 cm depths. Thin sections of the sand fraction (Figure 3) of the lower parts of the profile show sharp-edged, relatively unaltered rock fragments, whereas sand at 0–5 cm had a higher degree of alteration. The sharp edges indicate the relatively low degree of soil development, as well as little movement. Less matrix material and single plagioclase fragments separated from the matrix, the latter occurring less frequently at depth, additionally indicate in situ soil development.
- The patterns of REE indicate that input of allochthonous material did not occur in the profiles in amounts large enough to affect REE pattern. If bedrock was the source for soil (i.e. bedrock and parent material are identical) the REE pattern in Figure 4 should show parallel lines and the same Eu anomaly throughout the profile (Kurtz et al., 2001). This is the case for most profiles, which even show ideal cases of the expected pattern (profiles 2, 4, 5, 6, 7 and 9). Solely for profile 1 we cannot completely rule out dust input, erosion or soil movement as some deviation from the ideal pattern was found. The Europium anomaly was still apparent and therefore, just as for profiles 3 and 8, it could also be derived from translocation processes during soil development (Caspari et al., 2006). With the REE pattern we cannot completely rule out dust input from local sources with the same signature. However, all profiles were dug proximate to each other (200 m) and profile 9 was the one with greater distance to the others (400 m). The latter profile already showed a different REE signature (lower Eu anomaly) compared to the eight other profiles and such signals would likely affect REE pattern if dust inputs had occurred in relevant amounts.

Due to the three lines of evidence (rock content, thin sections of the sand fraction, REE signature of bedrock and soil) we conclude that all of the chosen profiles developed *in situ* and did not receive major material input by allochthonous sources. Hence, the chosen sites and profiles are well suited for studying *in situ* pedogenesis with and without land use.

4 Soil description

In the following paragraphs soils will be described according to the key of the IUSS Working Group WRB (2007). Thereafter, results of this study are discussed in context with other published studies.

Organic layers were present on pristine sites, especially in forest plots. However, a dense root mat overlaid the mineral soil; this pattern did not fully fit the definition of an O-layer, although organic fragments and pellets of mineral soil (probably worm casts) were intermixed into the roots. All profiles were characterized by having a thick mineral A-horizon overlying an R- (bedrock) or thin (< 5 cm) CB- over R-horizon (Figure 2, c, f and i). The CB-horizons were found exclusively in rangeland soils and may eventually develop into Bw-horizons given enough time. In fact, B-horizons were frequently found in valleys that appear more humid in comparable landscape positions on glacial till (personal observation). Organic carbon contents (Figure 5) were lower than required for 'organic material' and classification as Histosols could be ruled

Table 3. Soil properties of the pristine and rangeland sites. Sum or mean (weighted by soil mass) of the whole profile (n = 3).

	Pristine		Managed		
	Forest	Grass	Rangeland	CV_P	$p<F$
WRB classification	lePHsolaar	lePHsolaar	leUMhdla	–	–
Munsell colour	2.5Y3/1	10YR3/2	10YR1.7/1	–	–
Structure	gr+wc	gr	cr	–	–
Fine roots (dm^{-2})	> 200	>200	50–200	–	–
Profile depth (cm)	30	32	37	± 44%	0.721
Soil mass ($kg\ m^{-2}$)	153	164	216	± 44%	0.529
SOC stock ($kg\ m^{-2}$)	16.3	15.3	21.6	± 30%	0.283
C/N ratio	16	14	15	± 7%	0.106
Base saturation (%)	95[a]	72[b]	23[c]	± 21%	<0.001
Al saturation (%)	1[a]	19[a]	75[b]	± 69%	<0.001
Sand (%)	78.3[a]	71.0[a]	60.5[b]	± 7%	0.009
Silt (%)	20.3[a]	27.0[a]	38.3[b]	± 18%	0.006
Clay (%)	1.4	1.9	1.2	± 41%	0.504
Texture class	LS	LS	SL	–	–

CV_P: pooled coefficient of variation; gr: granular; wc: wormcasts; cr: crumbly; LS: loamy sand; SL: sandy loam.

out. Depth of the A-horizon comprised, as a mean, between 30 cm and 37 cm (Table 3). Profile depth did not differ significantly ($p = 0.721$) between vegetation types and was highly variable (CV = 44%). Soil depth was higher and rock content lower as required for classification as Leptosol. The following eight Reference Groups in the key were clearly ruled out, due to lack of high clay content (Vertisol, Solonetz), direct anthropogenic impact (Anthrosol, Technosol), ice (Cryosol), fluvial material (Fluvisol), readily soluble salt (Solonchak) or reducing conditions (Gleysol). Occurrence of Andosols was possible, as reported before for parts of the Andes (Hofstede, 1995). Soils require andic or vitric properties to qualify as Andosols. Low bulk density (< 0.9 g cm^{-3}), high phosphate retention (85%) and Fe/Al chemistry are criteria for andic properties. The proportion of $Al_o + {}^1/_2Fe_o$ has to be higher than 2%, which was not the case (Table 4). The value was, however, larger than the 0.4% required for vitric properties in the rangeland profiles. Nevertheless, vitric properties require volcanic glass in the sand fraction, which was not present. The next Reference Groups were ruled out because soils did not have spodic (Podzols), plinthic (Plintosols), nithic (Nitisols) or ferralic (Ferralsols) horizons and lacked stagnic colour patterns (Planosols, Stagnosols).

Due to accumulation of organic matter and a high base status in pristine soil profiles, mollic horizons were identified. Five criteria must be fulfilled for the identification of mollic horizons: (1) a sufficient soil structure that the horizon is not both massive and hard when dry; (2) Munsell colours with chroma < 3 when moist and a value < 3 when moist or < 5 when dry; (3) SOC $\geq$ 6 g kg^{-1} or SOC $\geq$ 25 g kg^{-1} when colour requirements are waived; (4) a base saturation of 50% or more and (5) a thickness of either 25 cm or more or 10 cm or more if overlying continuous rock. Whereas pristine soils meet all the criteria, rangeland soils solely fail to meet the requirement for high base saturation. Consequently, an umbric horizon was identified for rangeland soils. Due to the absence of cementing materials or clay illuviation, rangeland soils were classified as Umbrisols.

Table 4. Chemical index of alteration for bedrock and soil as well as extractable forms of Fe and Al and derived indices as indicators for soil development. Means for the entire A-horizon (n = 3).

	Pristine		Managed		
	Forest	Grass	Rangeland	CV_P	$p<F$
Chemical index of alteration (CIA)					
Bedrock (mol mol^{-1})	58.0	58.2	60.7	± 4%	0.309
Soil (mol mol^{-1})	56.0[a]	58.9[a]	66.2[b]	± 6%	0.015
Change (%)	−1.4[a]	0.7[a]	9.3[b]	± 166%	0.002
Pedogenic forms of Fe and Al					
Fe_d (g kg^{-1})	7.3	9.2	13.7	± 31%	0.196
Fe_o (g kg^{-1})	2.6	4.5	5.6	± 29%	0.071
Fe_p (g kg^{-1})	1.1	2.5	3.3	± 34%	0.051
Al_o (g kg^{-1})	1.2[a]	2.6[a]	8.9[b]	± 29%	<0.001
Al_p (g kg^{-1})	0.7[a]	1.7[a]	5.6[b]	± 34%	<0.001
Pedogenic oxide ratios					
Fe_d/Fe_T	0.24[a]	0.26[a]	0.33[b]	± 7%	0.002
Fe_p/Fe_T	0.04	0.07	0.08	± 30%	0.086
Fe_o/Fe_d	0.34	0.44	0.44	± 20%	0.343
Fe_p/Fe_o	0.45[a]	0.53[b]	0.59[b]	± 10%	0.039
Al_o/Al_T	0.02[a]	0.04[a]	0.12[b]	± 24%	<0.001
Al_p/Al_T	0.01[a]	0.03[b]	0.08[c]	± 31%	<0.001
Al_p/Al_o	0.59	0.62	0.64	± 8%	0.531

CV_P: pooled coefficient of variation.

Pristine profiles with a mollic horizon could potentially be classified as Chernozem, Kastanozem or Phaeozem. Since the former two require a calcic horizon, pristine soils were classified as Phaeozems. All soil profiles had continuous rock within 1 m depth and receive the prefix 'Leptic'. Pristine sites had textures of loamy sand and receive the suffix 'Arenic'. Moreover, high proportions of exchangeable Mg (Mg + Na > 15%; Figure 6) on the exchange complex led to classification as 'Sodic'. The base saturation of the rangeland soil was below 20% justifying the 'Hyperdystric' suffix. Although not specifically listed for the Reference Soil Groups Umbrisol and Phaeozem, the suffix 'Laxic' ($\rho < 0.9$ g cm^{-3}) seems important to describe all soils. Hence, pristine soils were classified as Leptic Phaeozems (Sodic, Laxic, Arenic) and those of the rangeland as Leptic Umbrisols (Hyperdystric, Laxic).

In general, soils of the high Andes within the moist puna or páramo biomes were described as carbon rich and acidic in nature (Alexander and Pichott, 1979; Hofstede, 1995; Miller and Birkeland, 1992; Wilcox et al., 1988). This notion fits well to the results of this study (Figures 2 and 5, Table 3). Moreover, bulk density was commonly very low, which was generally attributed to the influence of volcanic material (Hofstede, 1995). Alexander and Pichott (1979), however, stated that low bulk densities were also a common feature of soils above 2000 m a.s.l. regardless of volcanic influence (Cordillera Oriental, Colombia). In our study area, animal trampling led to compaction of the top 20 cm in rangeland soil, which is in agreement with data of other studies (Hamza and Anderson, 2005; Hofstede, 1995). Compared to other studies (Miller and Birkeland, 1992; Wilcox et al., 1988), the soils we encountered are relatively weakly developed, which is

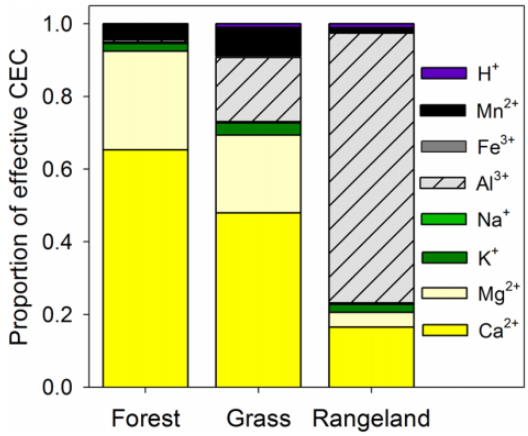

Figure 6. Proportions of different cations on effective cation exchange capacity (CEC). Soil-mass-weighted mean values (n = 3) of the whole A-horizon. Proportions of Na^+ and $Fe3^+$ are too small to be recognized.

shown by the shallow profile, lack of a B-horizon and low clay contents (1.2–1.9%, Table 3). Soils of this study are also (presumably) rather young. Although signs of direct glaciation are below the landscape position of the profiles, periglacial conditions must have been rather harsh. We presume that any existent soil or saprolith was eroded from the slopes and soil development started anew with the onset of vegetation cover. As a rough estimation, soils are younger than 10–5 kyears, a range also given for soils developed on glacial till near the study region (Miller and Birkeland, 1992; Wilcox et al., 1988). These soils were described as somewhat deeper as in this study and B-horizons with clay illuviation were identified. Soil development on glacial till, however, should be faster compared to development on continuous bedrock, due to higher amounts of fine-grained particles which increase surfaces available for chemical reactions (Gabet and Mudd, 2009). Weathering resistant bedrock may also explain the low clay contents: one profile described by Wilcox et al. (1988) developed on an andesitic colluvium (footslope) and exhibited much lower clay content (c. 10%) compared to glacial till (20–50%). In the Alps (1760 a.s.l.), Egli et al. (2001) reported similarly low clay contents (0.7–2.4%) in a 10 kyear old Haplic Podzol developed on granitic parent material. Moreover, the semi-humid sites in this study are northwest-exposed (Southern Hemisphere), which generally promotes evapotranspiration and inhibits profile development compared to shaded, moister slopes (Birkeland et al., 2003). The low degree of development is typical for high mountain soils of the Andes (Zech and Hintermaier-Erhardt, 2002) due to the rather short time of development (glacial retreat c. 15–10 ka ago; Zech et al., 2009), the cool climate and the pronounced dry season.

Overall, the general features of the soils described in this study fit the limited observations from the study region (Miller and Birkeland, 1992; Wilcox et al., 1988). Although located on steep mountain terrain, Miller et al. (1993) reported by using ^{14}C measurements that slopes were quite stable during the Holocene, i.e. the period of soil development was also stable. It should be noted that the present study does not intend to describe common soil types of the study region, which is also characterized by glacial till, alluvial fans and slope debris, but to find sites with in situ soil development to quantify the influence of the human state-factor. Although all soils had many features in common, rangeland and pristine soils were classified differently due to their opposing state regarding exchangeable bases and Al. Despite being grouped into different Reference Groups of the IUSS Working Group WRB (2007) and not just qualifiers (the prefixes and suffixes of the Reference Group), one may argue that different base status is a minor effect for millennia of anthropogenic influence. Soil genesis was, however, not very advanced, which impedes larger differentiation per se and more pronounced human impact was unlikely as grazing management

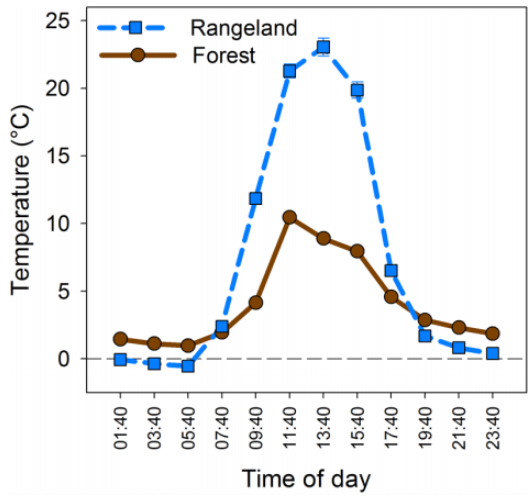

Figure 7. Daily temperature course as means with standard errors over 326 days in 2011/2012 at the soil surface. Loggers were placed in forest and rangeland plots.

in the region, even with its long history, is not, and is unlikely to ever have been, very intensive.

5 State of weathering

The soil texture and the thin sections of the sand fraction indicate differences in the state of physical alteration. For instance, the proportion of sand is significantly higher in forest and grass soils (78.3 and 71.0%, respectively) compared to rangeland soils (60.5%, Table 3). Since we ruled out relevant deposition of aeolian material (Figure 4), coarser texture of pristine soils may only be explained by two processes: depletion of fines on the pristine sites by wind erosion or advanced physical alteration on rangeland sites. On the one hand, wind erosion on pristine sites does not seem likely, regarding the vegetation cover, which protects the soil surface well (Table 1, Figure 2), especially when compared to rangeland sites. On the other hand, a diurnal temperature amplitude of 24 K on rangeland compared to 11 K on forest sites (Figure 7) may enforce physical weathering (insolation) in rangeland soils. Similar patterns for temperature amplitudes and daily mean temperatures were reported by Rehm and Feeley (2013) for forest patches, open puna and forest edges for sites c. 100 km northeast of our site (3200–3600 m a.s.l., Manu National park). In our study, no loggers were placed in clearings, but the results of Rehm and Feeley (2013) indicate a moderate daily temperature amplitude settled between values of open puna and closed forest. In addition to the insolation effect, constant animal trampling (see animal tracks in Figure 2g) could have resulted in the mechanical breaking up of soil material to form smaller particles. While soil compaction by animal trampling is well known (see review by Hamza and Anderson, 2005), there is no literature available on the effects of trampling on soil texture. This effect, although quite possible, therefore remains speculative. Besides containing a hint on physical alteration, the thin sections show that the sand fraction is mainly composed of small, sharp-edged rock fragments with primary minerals. This indicates that chemical weathering is not very advanced. Higher physical breakdown, however, may facilitate chemical weathering (Gabet and Mudd, 2009; Schlesinger and Bernhardt, 2013).

The CIA indicates the loss of Na, Ca and K relative to Al, which mirrors feldspar weathering (Buggle et al., 2011; Nesbitt and Young, 1982). Since CIA values of bedrock varied slightly, albeit not significantly, in this study, a change of CIA in soil relative to bedrock was calculated. In pristine soils, values were not significantly different from zero (t-test, $p \leq 0.05$, Table 4), whereas CIA increased by 9.1% in rangeland soils. This, in general, indicates the low degree of chemical weathering and/or little leaching of elements. For example, Yang et al. (2006) showed that the CIA in the sand fraction of Chinese loess soils was about 60 and increased gradually with decreasing grain size to 80 in the clay fraction, showing that chemical weathering was associated with clay formation. Caspari et al. (2006) presented CIA values around 80 for soils

in Bhutan (1500–3800 m a.s.l.). Due to the polygenesis of soils, however, it was difficult to assign baseline values for parent material. Moreover, transformation does not necessarily mean translocation if leaching is low, which might be the case under semi-humid to semi-arid conditions. Therefore, pedogenic oxides were analysed to indicate transformation processes.

The Fe_d contents ranged from 7.2 to 13.7 g kg^{-1} and did not differ significantly (Table 4). As a proportion of total Fe (Fe_d/Fe_T), however, rangeland soils showed significantly higher proportions of pedogenic Fe (0.24, 0.27 and 0.33 in forest, grass and rangeland soil, respectively). The relatively low proportions indicate pedogenesis during the Holocene and are well comparable to values by Egli et al. (2001) for alpine Podzols (10 kyears, granitic parent material, 1760 m a.s.l.). The ratio of Fe_o/Fe_d, representing the degree of crystallization of pedogenic Fe-oxides, has been used to evaluate the state of weathering, assuming a higher degree of crystallization with age, i.e. development (Torrent et al., 1980). In this study, the Fe_o/Fe_d ratio did not differ significantly. If seen as an indicator for soil age (Torrent et al., 1980), this is consistent with our assumption that pedogenesis commenced at the same time on all sites. Although weathering (as indicated by the Fe_d/Fe_T-ratio) was significantly faster in rangeland soils (see also discussion below), the same proportion of pedogenic Fe-oxides crystallized. The Fe_o/Fe_d-ratio can be affected by vegetation cover, presumably due to specific properties of SOM derived from certain vegetation types. It has been shown that grass vegetation inhibits and forest vegetation promotes crystallization of Fe-oxides, presumably due to complexation of Fe and SOM (Dümig et al., 2008). In our study, this was indicated by a trend (Table 4, $p = 0.051$) of higher Fe_p contents and a significantly higher Fe_p/Fe_o ratio under grass-dominated vegetation (managed rangeland and pristine grass).

Although significant, the difference of the Fe_d/Fe_T ratio between managed and pristine soils was relatively small. Pedogenic forms of Al showed much more pronounced effects (Table 4). For instance, Al_o concentrations were 3.4 (grass) to 7 times (forest) higher in rangeland soil. Similar marked differences were found for Al_p concentrations and the corresponding proportions Al_o/Al_T and Al_p/Al_T. The higher release of Al by weathering is also reflected in the proportion of Al^{3+} on the CEC (Table 3, Figure 6). The ratio of $Al_p/Al_o > 0.5$ indicates that Al is strongly associated with SOM (IUSS Working Group WRB, 2007; Vacca et al., 2009). Although the formative element 'aluandic' (Alp/Alo > 0.5, also called non-allophanic) is in the World Reference Base reserved for Andosols, it was pointed out that Al-SOM-complexes may be relevant for non-Andosols (Dümig et al., 2008; Vacca et al., 2009). For instance, Dümig et al. (2008) reported the outstanding importance of Al-SOM-complexes in the genesis of highly weathered Umbrisols in southern Brazil. High proportions of Al-SOM-associations may explain the very high SOC concentrations encountered in all soil profiles of this study.

Summarizing the findings above, rangeland soils exhibited a state of more intense physical and chemical weathering compared to pristine forest and grass soils. This was also shown by Price et al. (2012) for Si weathering comparing watersheds with different proportions of forest and agricultural land. Since SOM is well known to be stabilized by organo-metallic interactions, the state of weathering may determine the level of organic carbon stored in soils.

6 Soil organic carbon storage

Stocks of SOC were not significantly different between the sites, although rangelands showed somewhat higher stocks, (21.6, 16.3 and 15.3 kg m^{-2} in rangeland, forest and grass soils, respectively; Table 3) due to (insignificantly) higher soil mass. Our finding corroborates the results of

Zimmermann et al. (2010) who showed no differences in SOC stocks of grassland and forests between 3000 and 3900 m a.s.l., close to our study site. A review by Tanentzap and Coomes (2012) showed that SOC stocks were not uniformly affected by grazing. Furthermore, in a meta-analysis Guo and Gifford (2002) showed a marginal mean increase of 8% in SOC stocks after conversion of forest to pasture.

Concentrations of SOC gradually decreased with depth, but were very high throughout the profiles (Figure 5). The mean for the forest plots in 0–5 cm was 211 g kg^{-1}. Bunchgrass and rangeland soils had lower concentrations of c. 135 g kg^{-1}. However, differences were not significant and converged down the profile to 55–77 g kg^{-1} in 30–40 cm depths. The high SOC concentrations compare well with the findings of Zimmermann et al. (2010) between 3000 and 3900 m a.s.l. (Manu National Park, c. 100 km northeast of our site) and correspond well to the decelerated soil genesis of the cold and semi-humid climate (Zech and Hintermaier-Erhardt, 2002). It has been shown that SOC concentrations in grassland decrease significantly by clipping and removing (as grazing simulation) above-ground biomass regularly (Lajtha et al., 2014). That this effect has not been observed may, on the one hand, be explained by increased root turnover on rangeland sites, which increases below-ground C-input (Bardgett and Wardle, 2003). Root input seems to favour build-up of SOC compared to above-ground C input (Rumpel and Koegel-Knabner, 2011), which, however, is a conclusion derived from short-term experiments that has been recently challenged (Lajtha et al., 2014). On the other hand, preservation of SOC may be explained by the changing importance of stabilization mechanisms: the finer texture in rangeland soils offers a higher specific surface area and more SOC can be stabilized compared to coarse-textured soils (Schleuß et al., 2014). Moreover, higher contents of organically complexed Al (Al_p, Table 4) indicate that this mechanism is of major importance to prevent SOC loss (Heitkamp et al., 2012; Stevenson, 1994; von Lützow et al., 2006).

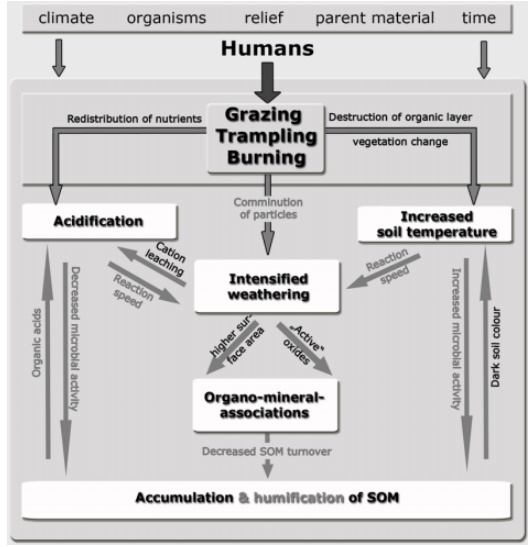

Figure 8. Model of interactive controls of and between weathering and SOC accumulation.

V Interactive controls of weathering and SOC accumulation

Based on the state-factor model, we present a model of interactive controls of and between weathering and SOC accumulation (Figure 8). We found slower processes of physical (insolation, animal trampling) weathering in the generally little developed soils under pristine vegetation. Anthropogenic vegetation change induced increases in soil temperature (Figure 7) and acidity (Figure 5, Table 3) that forced a positive feedback loop in rangeland soils. Chemical weathering was enhanced by the higher surface area (less sand, Table 3) and higher soil temperature (Figure 7). Advanced weathering rendered elements susceptible to leaching; the higher loss is indicated by the higher CIA (Table 4) and by the exchangeable cations (Figure 6). Loss of cations may be enhanced by nutrient exports by animals. This can be seen as an amplifying control: weathering promotes acidification and vice

versa. The intensified weathering in rangeland soils possibly gives way to SOC preservation, mainly in Al-SOM complexes (Kleber et al., 2005). The finer texture of rangeland soils probably increased this effect (Heitkamp et al., 2012; Schmidt et al., 2011), although this cannot be proven yet by our data. Accumulation of SOC and humification is accompanied with the presence of organic acids (Stevenson, 1994), which feeds back to acidification. Acidification in turn decreases microbial activity (Swift et al., 1979), slowing down decomposition. However, this is in contrast to a potentially increased microbial activity caused by increased temperature (Davidson and Janssens, 2006), provided there is sufficient soil moisture (Swift et al., 1979). Nevertheless, protection from mineralization by complexation and/or sorption slows down turnover of SOM (Heitkamp et al., 2012; von Lützow et al., 2006) and, hence, proportions of more humified SOM will be higher. A stronger degree of humification may, therefore, be responsible for the darker soil colour (Figure 2, Table 3) in rangelands which, in turn, amplifies the temperature increase due to sparse vegetation cover (Table 1).

Some of the presumed processes involved in the feedbacks have to be confirmed by further analysis and the presented model of anthropogenic effects on soil development has to be tested for more general validity. It is open to question if this feedback loop will be valid under different conditions, such as different climate, vegetation, relief, parent material or time of soil development. Moreover, a different land-use, such as more intensive cropland, may have more pronounced effects. It should be noted that, even on steep slopes, erosion seemed to be of minor importance, as also indicated by Miller et al. (1993). This may well be different at locations with less precipitation, where plant cover and SOC concentrations are lower (Maetens et al., 2012). For instance, Coppus et al. (2003) showed that erosion was a relevant process in semi-arid locations of southern Bolivia.

VI The use of inaccessibility as a tool

Our case study analysed soil development in the puna region of the tropical high Andes. We were able to clearly isolate the human influence on soil and derive a model about the processes and their feedbacks on soil (Figure 8), which were triggered by vegetation change and animal trampling. It has already been shown that inaccessibility can be used as a useful tool to identify the potential natural vegetation of areas of the puna where grazing exclosure experiments are not in place (Sylvester et al., 2014). Our research shows that inaccessible ledge habitats can be used to infer the potential natural soil conditions of areas of the puna that are heavily impacted by anthropogenic pressures, as is the case almost everywhere.

The challenge now is to apply the tool of inaccessibility to other localities, where state-factors are different. This includes areas with differing classical factors of climate, organisms, relief, parent material and time, but especially areas with a differing archaeological, historical, cultural and technological component of the human factor. Including more sophisticated methods such as isotopic or trace elements analysis to quantify weathering rates and measurement of element fluxes, such as carbon cycling or chemical mass balances, will enable us to use the proposed model more quantitatively, as recently proposed for the state-factor 'time' and the relation between pedogenesis and plant species richness (Laliberté et al., 2013).

Of course, the tool, as every other tool, has its drawbacks. Obviously, pristine sites will mainly be found in mountain ecosystems or extremely remote areas. In remote areas, it may be hard to find comparable sites with human impact, whereas in mountainous regions, the land-use practices are often restricted. Nevertheless, having such a tool available in mountain ecosystems is still valuable, because elevational gradients reflect (again not without restrictions)

the global latitudinal patterns of climates and ecosystems (Malhi et al., 2010; von Humboldt and Bonpland, 1805). It should also be taken into account that atmospheric deposition and climate change are anthropogenic alterations that are affecting even the most remote and inaccessible locations meaning that the baseline values obtained may not reflect past natural soil conditions. Nevertheless, in the absence of palaeoecological data, experimental approaches using inaccessible soil conditions as baseline data are the most objective way for looking at anthropogenic influence on soil development.

This study justifies 'humans' as a soil and ecosystem forming factor and validates that 'inaccessibility' can be used as a suitable tool to assess the human impact on soil development. We propose to combine our methodological approach with other scientific disciplines, such as palaeosciences (Kiage and Liu, 2006), anthropology (Isendahl, 2010) and historical ecology (Balée, 2006), and apply it in the framework of the state-factor model (Amundson and Jenny, 1997; Jenny, 1941). We are confident that interdisciplinary, rigorous use of this tool will be a step forward in quantifying regionally valid thresholds and landscape sensitivities, which will help in defining a 'safe operating space for humanity' (Rockström et al., 2009).

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Author Contributions

Conceived the field design: MK, SPS; conceived and designed the soil study: FH, HFJ; performed fieldwork: SPS, FH, MDPVS; analysed soil samples and data: FH; wrote the manuscript: FH, HFJ, SPS, MK.

Declaration of Conflicting Interests

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Chapter 3

Shifting perspectives on naturalness in mountain ecosystems

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Shifting perspectives on naturalness in mountain ecosystems

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How have millennia of human landuse modified high mountain ecosystems? Until now, researchers have been unable to obtain data from truly undisturbed ecosystems to address this question. Here we provide the first example of real-time baseline data, based on current ecological conditions, of vegetation and soil from pristine relict ecosystems in the Peruvian Andes. N**atural ecosystems were fundamentally different from previously known Andean ecosystems, having ca. 10 times more forest, greater biomass, lower alpha but higher beta plant diversity, and being largely comprised of species new to science and with restricted ranges. Soils were mainly influenced by transformation of forest to grassland, with relatively little degradation within these vegetation types. This provides novel baselines to address questions on human impact and sustainable management in mountains.**

Keywords:, alpha- beta- diversity, carbon stocks, anthropogenic impact, introduced species, soil, restoration, shifting baseline syndrome

Humans have affected ecosystems to such a degree, and over such long time periods, that it is nowadays almost impossible to obtain baseline values from undisturbed ecosystems to assess past and present anthropogenic influences (Amundson and Jenny 1997; McMichael et al. 2012). Evidence is accumulating that early human activities, especially that of expanding Neolithic populations, had a fundamental impact on the vast majority of environments across the globe, creating man-made landscapes with vegetation and soils different to what would naturally occur (Ellis et al. 2013). It is now feared that a shifting baseline syndrome is under way in our societies, with perceptions of what is "natural" becoming biased towards anthropogenically disturbed ecosystems (Papworth et al. 2009). Researchers have tried to counteract this through the use of historical ecological data from ecosystems prior to human arrival to infer baselines. This approach, however, is problematic based on the applicability and quality of the results (Jackson & Hobbs 2009; Miehe et al. 2014), as well as the ecosystem properties that can be quantified. Despite these drawbacks, current understanding of human impact on Earth's ecosystems stems largely from paleoenvironmental proxies, which has often created debate regarding natural ecosystem states due to inconsistencies with ecological research.

This is never more apparent than with regards high mountain ecosystems. Nowadays, these ecosystems are largely composed of grassland (3,851,309 km^2, Dixon et al. 2014), but palynological and ecological evidence suggests that forests once covered a large proportion of many highlands, and suffered drastic declines in the late Holocene (Hansen 1994; Herzschuh et al. 2010; White 2013; Miehe et al. 2014). Some researchers argue that these declines can be attributed to climate change and that current forest distributions are natural (Gosling et al. 2009; Herzschuh et al. 2010), whilst others point to human impact as the main culprit (Wesche et al. 2000; Kessler 2002; Miehe et al. 2009, 2014; White 2013). In the Andes, humans are known to have been present above 4,000 m.a.s.l. since as far back as 12,800 years ago (Rademaker et al. 2014). The challenge here is discerning causality in a situation of concurrent climate change, human expansion and forest decline.

It becomes obvious that there is a real need for ecological baselines that are free from the methodological drawbacks associated with historical ecological data. In exploratory studies, we validated that zonal vegetation on mountain ledges, only accessible using mountaineering equipment, can be used to infer potential natural vegetation (Sylvester et al. 2014) and soil development (Heitkamp et al. 2014) of the high Andean puna ecosystem. In the present study, we used remnants of natural vegetation on extensive mountain ledges in the Peruvian high Andes to infer real-time baselines based on current ecological conditions.

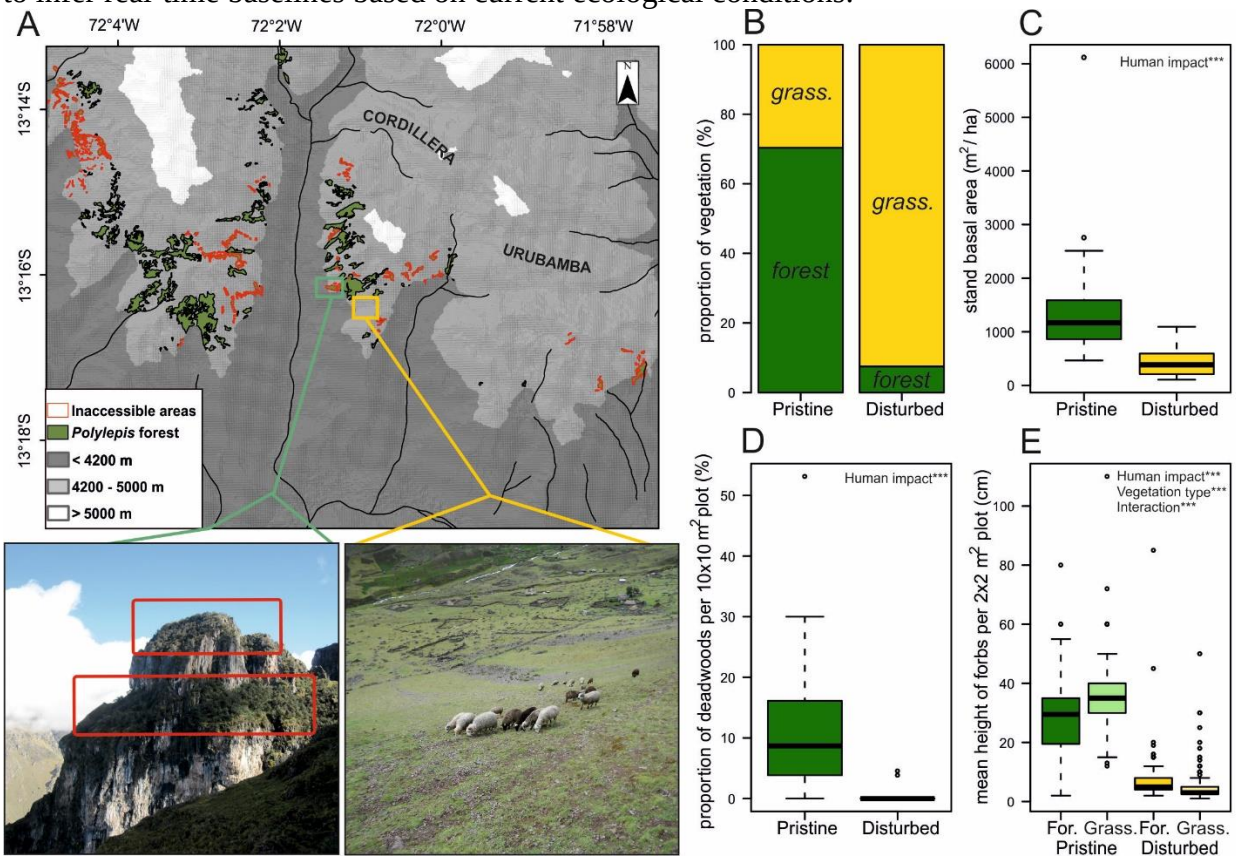

Fig. 1. Comparisons of pristine and disturbed vegetation structure (A-E). Example of the landscape mapping approach showing a pristine and nearby disturbed site (A)**.** Comparisons of the proportion of forest and grassland of zonal vegetation in the Cord. Urubamba between 4200 m and 4900 m (B), stand basal area (C) and proportion of deadwoods per forest plot (D), and mean height of herbaceous vegetation per plot (E). Significant relationships between the structural properties and fixed effects found upon analysis using generalised linear mixed models (GLMM's) are noted within the plots (***=p<0.001; Table S4-5). Sample size for C, D: Pristine forest 25, Disturbed forest 23; E: Pristine forest 160, Pristine grassland 83, Disturbed forest 118, Disturbed grassland 111.

In a first step, we applied landscape mapping based on high resolution Bing and Landsat 8 satellite images focusing on elevations above 4200 m in the Cordillera Urubamba, over an area of 132,660 km^2 (Fig. 1A, S1). Areas of pristine zonal vegetation occupied only 1.1% of the surface, whilst 56.9% was disturbed zonal vegetation, with the remaining 42% corresponding to azonal habitats such as landslides, rock faces, glacial moraines, stream margins, and bogs. Disturbed zonal vegetation had 90% less forest cover than natural vegetation (Fig. 1B, Table S2-3) implying a transition from forest- to grassland-dominated ecosystems at the landscape scale. Our study, alongside other ecological research (e.g. Kessler 2002; White 2013; Sylvester et al. 2014), refutes the idea that the current distribution of small scattered relict woodlands, restricted to inaccessible areas in the high Andes, is natural. Instead, we show that human impact is the main culprit for the current dominance of grassland and that a forest-grassland mosaic would dominate large proportions of the high Andes if humans had not encroached on this landscape.

We then compared disturbed and pristine forest structure using 48 10x10m^2 forest plots, and plant diversity and composition using 472 2x2m^2 plots, from the Cordilleras Urubamba and Vilcabamba (Fig.S1). Pristine habitats contained denser forests, with larger trees, and more standing deadwood (Fig. 1C-D, Fig. S4) as well as denser and taller herbaceous plant communities (Fig. 1E, Fig. S5). These differences reflect the impact of human-related grazing, timber extraction, and burning (Wesche et al. 2000; Toivonnen et al. 2011, White 2013). Pristine habitats had lower vascular plant alpha diversity compared to disturbed habitats (Fig.2A) due to dominance by a few highly competitive species. Despite the low alpha diversity, pristine habitat types contained more species with restricted range sizes (Fig. 2E) and had higher beta diversity (species turnover) between sites, especially for pristine grassland (Fig. 2B). Most importantly, the dominant species in the herbaceous vegetation of pristine habitats were mostly species new to science (Fig. 2C, Fig. S6, Table S8). Pristine forests were particularly important as hosts for these 'new' species, with 25% of species highlighted as indicators for this vegetation type being undescribed (Table S8-10, supplementary online text). Anthropogenically disturbed vegetation, in contrast, had a greater proportion (Fig. S6) and cover (Fig. 2D) of introduced species per plot, and was dominated by widespread generalist species (Fig. 2E, Table S9-10), most of which had adaptations to human-induced burning and grazing (Fig. 2G, S7-8, Table S12-13, supplementary online text). Natural herbivore grazing would occur in the Andes, but this would be less intensive than current grazing levels and would not support the short grazing lawns currently found across the majority of the landscape (Cingolani et al. 2014). This raises the question over the origin of the lawn flora. Based on ad hoc observations, we suspect that species associated with disturbance are found in azonal habitats within the natural vegetation matrix.

After observing noticeable differences in epiphytic lichen communities between living and standing deadwood trees, which were not present in disturbed forests due to firewood extraction by local people, we studied the diversity and composition of epiphytic lichens on these trees. The deadwood substrate had a unique and highly diverse (Fig. 2F) epiphytic lichen flora, with indval analyses retrieving 28 indicator species for deadwoods but none for live trees (Table S11). This unique and diverse lichen epiphyte flora was not found on live trees due to the peeling bark characteristic of the dominant *Polylepis* trees. Deadwoods are known to be important for ecosystem conservation in other parts of the globe (Sverdrup-Thygeson et al. 2014) and we show here that they enhance cryptogam diversity in Andean forest ecosystems. They are also likely to have other benefits, e.g., for invertebrates and birds, of which *Polylepis* forests harbour a high number of endemic and threatened species (Gareca et al. 2010).

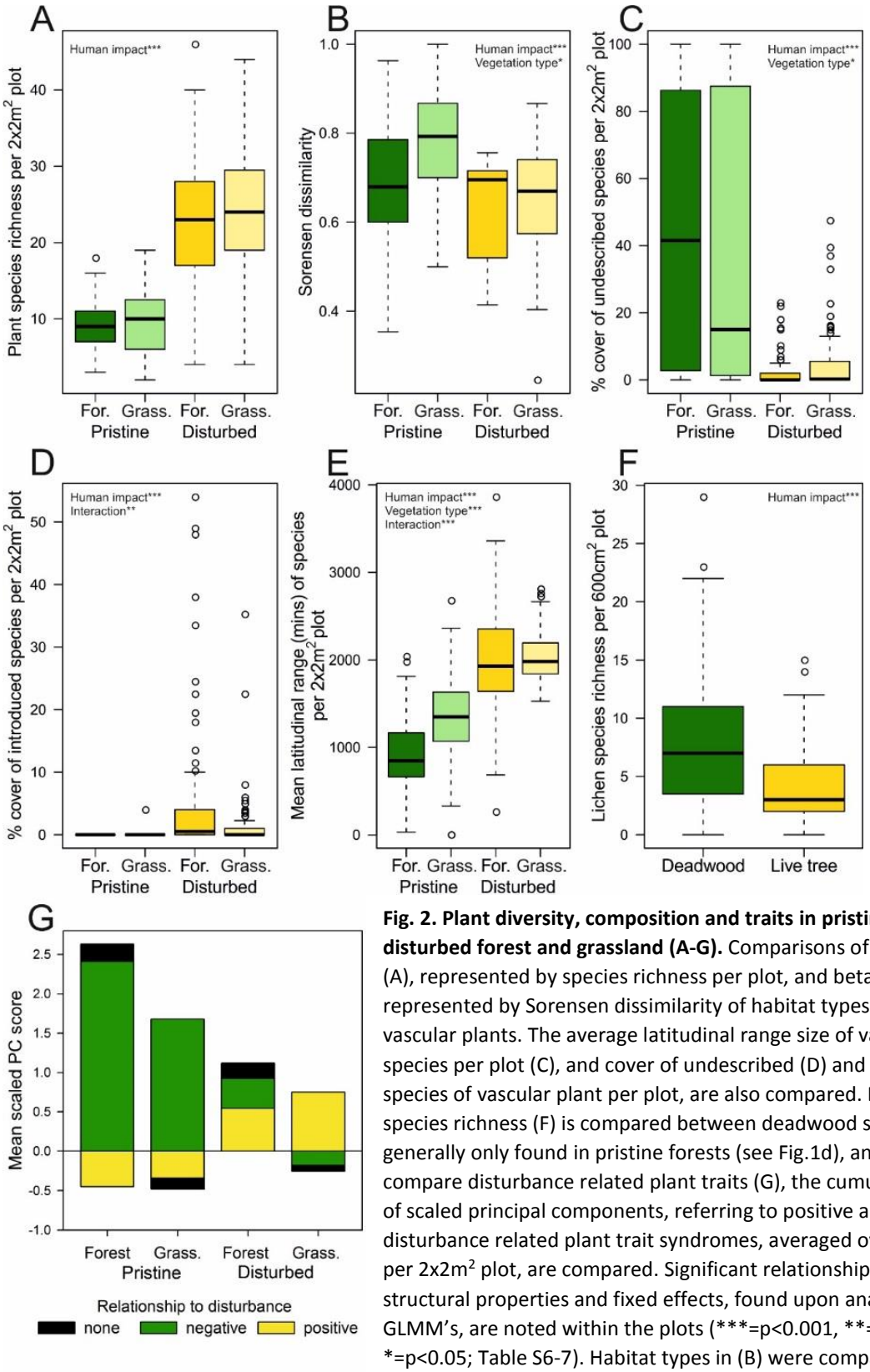

Fig. 2. Plant diversity, composition and traits in pristine and disturbed forest and grassland (A-G). Comparisons of alpha diversity (A), represented by species richness per plot, and beta diversity (B), represented by Sorensen dissimilarity of habitat types across sites, of vascular plants. The average latitudinal range size of vascular plant species per plot (C), and cover of undescribed (D) and introduced (E) species of vascular plant per plot, are also compared. Epiphytic lichen species richness (F) is compared between deadwood substrate, generally only found in pristine forests (see Fig.1d), and live trees. To compare disturbance related plant traits (G), the cumulative means of scaled principal components, referring to positive and negative disturbance related plant trait syndromes, averaged over all species per 2x2m^2 plot, are compared. Significant relationships between the structural properties and fixed effects, found upon analysis using GLMM's, are noted within the plots (***=p<0.001, **=p<0.01, *=p<0.05; Table S6-7). Habitat types in (B) were compared using two-way ANOVA with interaction followed by Tukey posthoc tests. Sample size for A,C,D,E,G: Pristine forest 160, Pristine grassland 83, Disturbed forest 118, Disturbed grassland 111; B: 112 (28 for each category); F: Deadwood 228, Live 179.

The structural and compositional differences between disturbed and natural vegetation largely agree with previous assessments of human influence on high mountain vegetation (Wesche et al. 2000; Kessler 2002; Miehe et al. 2009, 2014; Toivonen et al. 2011; White 2013), but the degree to which humans have affected the high Andean vegetation is astonishing. In particular, the dominance of previously unknown species in natural ecosystems would – by definition – have been impossible to predict based on studying purely the disturbed vegetation. Likewise, although the degree to which anthropogenic activities homogenize vegetation is currently debated (McKinney & Lockwood 1999; Ellis et al. 2012), our baseline study shows that human activities have led to a homogenization of the Andean vegetation.

We then assessed soil parameters for the different habitat types in four areas in the Cordillera Urubamba. Unexpectedly, soil properties were not found to differ much between pristine and disturbed habitats, but were mainly influenced by the vegetation type. Most forest soils were Phaeozemes (9 of 10 on pristine sites, 5 of 6 on disturbed sites), whereas grassland soils were mostly Umbrisols (7 of 11 on pristine sites, 10 of 12 on disturbed sites)(Table S14, supplementary online text). Landscape change is often also soilscape change (Mikkelsen et al. 2007) because vegetation structure, including the rooted zone, affects ecosystem properties such as microclimate and matter fluxes. Forest vegetation functions as a "base pump" with tightly closed cycles of the most important nutrients (da Silva et al. 2011). In our case, this effect was reflected in the exchangeable cations Ca and Mg (Fig. 3A) that were more abundant in forest. Grassland, on the other hand, had lower demands of these nutrients by the vegetation (Jobbágy and Jackson 2004), lower evapotranspiration, and a lack of interception of precipitation (Farley et al., 2005; Foley et al., 2003). This led to depletion of Ca and Mg, whereas less mobile cations, such as Al^{3+}, were relatively accumulated. On the other hand, a reduction in pH-values, which would increase Al-solubility, did not occur (Fig. 3B). Nitrogen, however, appears to have been lost preferentially in grazed grassland, as indicated by a trend of increasing $\delta^{15}N$ values (Fig. 3C) (Høgberg, 1997). Isotopic signatures are, however, an integrated indicator for the N cycle, and the process leading to relative enrichment of heavy isotopes warrants further investigation

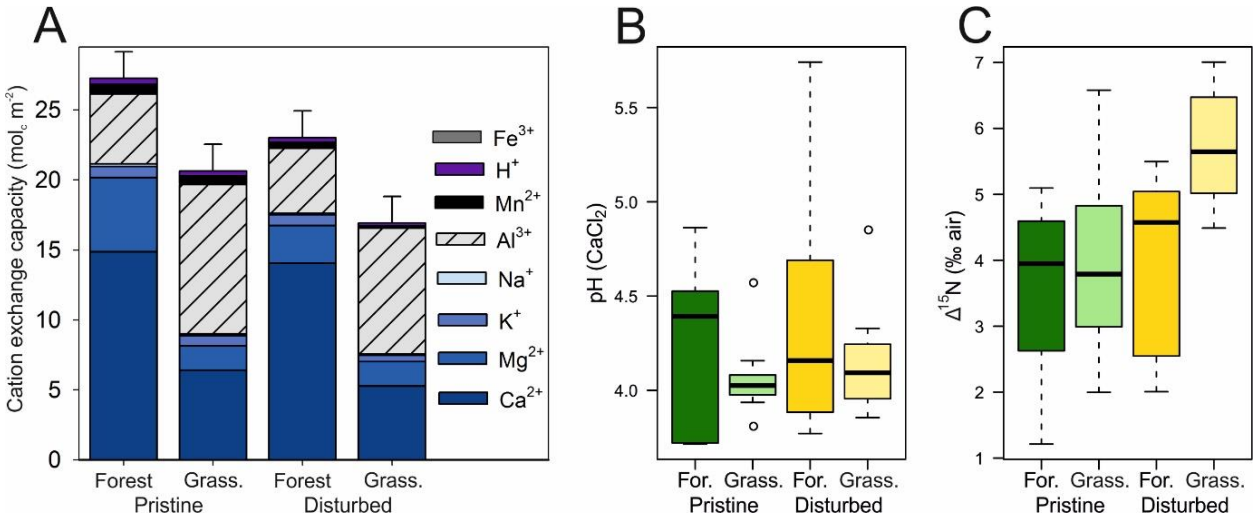

Fig.3. **Comparisons of soil nutrient properties between pristine and disturbed forest and grassland (A-C).** Comparisons of different minerals (A), pH (B), and ^{15}N concentration (C). Analysis with linear mixed models found no significant relationship with human impact was found for any of the properties apart from Na, whilst Al, Nt, Ca, Mg had a significant relationship with vegetation type (Table S15). Sample size (soil profiles): Pristine forest 10, Pristine grassland 11, Disturbed forest 6, Disturbed grassland 12.

(Amundson et al. 2003; Robinson 2001). Soil organic carbon (SOC) stocks were also found to be affected mainly by vegetation type, being 33% higher in grassland compared to pristine forests (Fig. 4C, Table S16-18). The increase of SOC in grasslands can be explained by its relation with short-range-order (SRO) minerals (Fig. 4B), which were more abundant in grassland. The importance of SRO minerals for SOC storage has been emphasised before (Masiello et al., 2004), especially in context with increasingly weathered soils (Kramer et al., 2012), but never before regarding long term human influence. This is the first demonstration that land use change can increase SOC storage in the long-term through increased concentrations of SRO minerals.

Therefore, human influence on soil nutrients was mainly indirect through conversion of forest to grassland which resulted in an opening of nutrient cycles. These results are in stark contrast to the general preconceptions of human impact on soils (Kaiser 2004). It is generally considered, largely from research based on low-elevation ecosystems, that pastoral practises lead to a depletion of available nutrients in the landscape, with local enrichment at resting or watering places (Dubeux et al., 2007; Kotzé et al., 2013). Our results highlight the resilience of high Andean soils to human impact and caution against generalisations regarding anthropogenic impact on soils. Considering the long grazing history of several millennia, the system may serve as an example of sustainable soil management.

Bringing vegetation and soils together, human influence thus had fundamentally different impacts on carbon stocks in the vegetation and soil components. Disturbed forests had on average 25% lower carbon stocks than pristine forests in trees, 49% lower in roots, and 18%

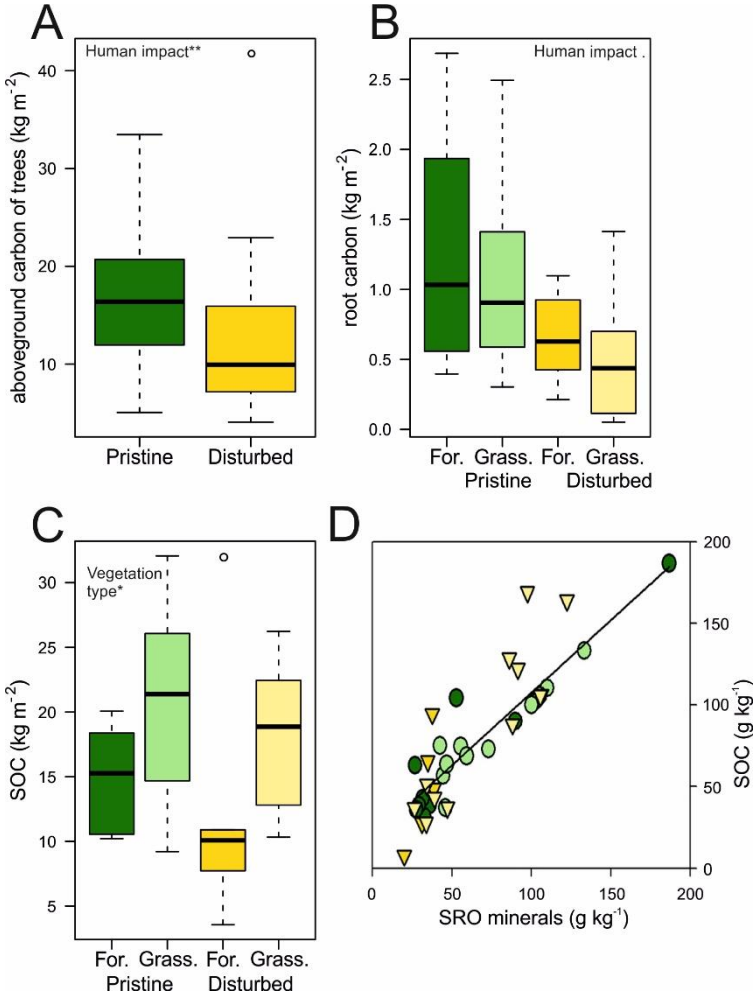

Fig. 4. Comparisons of carbon properties between pristine and disturbed forest and grassland (A-D). Comparisons of carbon contents in aboveground biomass of trees (A), root biomass (B) and Soil Organic Carbon (C). The positive relationship between SRO minerals and SOC (D; SOC = 13.5 + 0.99 SRO; R^2 = 0.78; $p < 0.001$) is shown with inverted triangles referring to disturbed grassland (light yellow) and forest (brown) and circles referring to pristine grassland (light green) and forest (dark green). The increase of SOC in grasslands was explained by its relation with short-range-order (SRO) minerals, which are more abundant in grassland. Significant relationships between the structural properties and fixed effects, found upon analysis using GLMM's, are noted within the plots (**=p<0.01, *=p<0.05, .=p<0.1; Table S16-17). Sample size of A: Pristine forest 25, Disturbed forest 23; B-D (soil profiles): Pristine forest 10, Pristine grassland 11, Disturbed forest 6, Disturbed grassland 12.

lower in soils (Fig. 4, Table S16-17). At a landscape scale, assuming that the pristine sites are representative of the variability in the landscape, transformation from forest to grassland further decreased tree and root carbon stocks by 90% and 58%, respectively, but increased SOC levels by 6% (Fig. S10, Table S18). These counteracting effects imply that, despite the massive increase in grassland, carbon stocks have only decreased by about 35% at the landscape scale (Table S19). The fact that human activity has a much lower effect on carbon stocks than commonly presumed is encouraging and means that, for conservation management focussing on carbon stocks in these high elevation ecosystems, the situation is not so dire. Nevertheless, forests should still be considered as important carbon stores in the high elevation puna biome (Vasquez et al. 2014).

Overall, our study highlights how human influence can cause tremendous shifts in ecosystem properties, but that these shifts are impossible to predict in the absence of baseline data. It is also important to note that human influence falls into two categories, namely degradation of a vegetation type and transformation from one vegetation type (forest) to another (grassland). These two processes can have contrasting effects, as most clearly shown by the decrease of SOC during degradation, but an increase during transformation.

The notion that the high elevation grasslands of the Andes are an artificial environment has implications, not only from a land management and conservation perspective, but also in our understanding of early human development in the Americas. By understanding the types of ecosystems that early hunter-gatherers encountered, we are now able to better understand human adaptations to these environments and the development of human cultures. With ample evidence of large-scale ecosystem degradation in the Andes even thousands of years ago (Thompson et al. 1988), indications for active reforestation activities in pre-hispanic times (Chepstov-Lusty et al. 2009) appear in a new light. Furthermore, current research on global climate change is heavily influenced by the results of paleoclimatic modeling which does not take into account the possible historical human impact on climate by large-scale modification of the vegetation and soils. Due to the sheer size of high-elevation biomes, radiation feedback effects mean that these biomes act as a high elevation heat sources which have a large influence on global atmospheric circulation (Feddema et al. 2005).

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Supplementary Materials for

Shifting perspectives on naturalness in mountain ecosystems

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This document includes:

Materials and Methods

1. Location and site conditions

The study was conducted in the Cordillera Vilcabamba and the Cordillera Urubamba of the Cusco region, in the southern Peruvian Andes (13° 08' - 13° 15' S, 72° 18' W, 4260-4830m a.s.l.) over 4 years between 2010-2014 (Fig. S1). The vegetation is classed as 'Puna' and is characterised by extensive tracts of tussock grassland interspersed with patches of *Polylepis* (Rosaceae) forest. The vegetation of the sites contained elements of flora characteristic of both the humid páramo, found in northern Peru (Marcelo Peña et al. 2006; Tovar et al. 2011), and the dry puna, which occupies the majority of the high elevation landscapes of central and southern Peru (Gutte 1987; Wilcox et al. 1986, 1987; Florez Martínez 2005).

All sites were characterised by low annual mean temperatures, a high diurnal temperature amplitude (Table S1) with a pronounced dry season from May to October. The Cordillera Vilcabamba sites were generally more humid than the Cordillera Urubamba sites due to receiving updrafts of humid air from the Amazon basin. Site 5, located at a mountain pass facing the Cordillera Vilcabamba, receives a large amount of humidity from updrafts of moist air passing across the pass and, thus, exhibits a vegetation and climate more characteristic of the Cordillera Vilcabamba. This difference in humidity is reflected by the recordings of mean annual precipitation in the closest climate stations which range from 454 mm in the Cordillera Urubamba (Urubamba, 2863 m a.s.l.) to 1606 mm in the Cordillera Vilcabamba (Winaywayna, 2800 m a.s.l.) (Toivonen et al. 2011). Since our study sites lie > c.1400 m above the climate stations, the data cannot be used to infer precipitation regimes at our study sites. Nevertheless, orography and vegetation pattern in the areas studied indicate that mean annual precipitation ranges at the higher end of these records. *In situ* records of air relative humidity and temperature for each Cordillera, averaging all datalogger sources (DS1923 Hygrochron iButtons), indicate that the Cordillera Urubamba sites generally experienced greater temperature variation, with colder extremes, and were generally drier (Table S1).

The pristine forest and grasslands were formed of zonal vegetation located on ledges ranging from c.0.2–1.5 km^2 in size. Inaccessibility was guaranteed by steep mountain cliff faces that inhibited access by grazing animals and blocked the spread of human-induced ground fires from the surrounding landscape. The accessible vegetation of the sites is subject to annual or biennial burning to remove undesirable tree saplings and old unpalatable tussock grasses, and to promote the resprouting of palatable new shoots. Animal trampling was widespread on accessible slopes, as typical for the whole region. Studies indicate that pre-Incan civilisations were present in the Cusco region for, at least, 4000 years (Chepstow-Lusty et al. 1996, 2000, 2009; Mosblech et al. 2012) and it is likely that these sites have been intensively used as rangeland during this time. An impression of the sites studied is shown in Figure S2.

2. Sampling Design

Pristine sites were selected based on their degree of inaccessibility and presence of zonal vegetation and differed from disturbed slope sites in being surrounded by cliffs that inhibited access to grazing animals and the spread of human-induced ground fires from the surrounding landscape. These sites were accessed using mountaineering equipment, either from above by controlled descents down the cliff faces, or from below using traditional climbing techniques. The accessible disturbed vegetation plots were located as close as possible to the pristine site, with the distance no more than ca. 500 m.

Pristine sites were comparable in most ecological conditions, especially the degree of soil and vegetation development, to disturbed slope sites and did not represent azonal vegetation, i.e., pure rocky area. This judgement was based on ledge sites having deep soils (>50 cm topsoil) with there being a lack of soil mass movements at all sites. All sites and plots were selected based on their having a similar exposition, elevation, microclimate and inclination, with these abiotic variables being controlled for as much as possible amongst the sites so that differences in vegetation could be attributed largely to the level of accessibility to anthropogenic disturbance.

2.1 Vegetation structure sampling design

2.1.1 Landscape mapping

We compared differences in forest and grassland cover in anthropogenically disturbed and undisturbed areas in the Cordillera Urubamba using a landscape mapping approach. Focusing on all areas in the Cordillera Urubamba above 4200 m (Fig. 1A, S1), we mapped forest cover on to high resolution Bing aerial satellite images within an ArcGIS platform. We then used a Landsat 8 satellite image based normalized difference vegetation index to select and extract areas without vegetation. Due to the coarseness of Landsat data, we also manually mapped over the extracted data to include azonal areas e.g. landslides, moraine, water bodies. Valley bottoms above 4200 m were delimited based on topographic information (ASTER Global DEM Version 2 of 30m) and were adjusted over the Bing aerial images. Grassland cover was then calculated by subtracting the cover data of forests and areas that were azonal without vegetation.

2.1.2 Forest structure sampling

Above ground stand structure was studied from disturbed and pristine forests above 3800 m in the Cordillera Urubamba and Vilcabamba (Fig. S1). In each forest, 10 x 10 m plots were recorded for all phanerophytes with a stem circumference greater than 10cm at breast height (130 cm from ground level), with the number of plots done being dependent on the stand size. Tree species, whether standing deadwood or live, dbh (diameter at breast height; 130 cm) and height were recorded for each individual tree or shrub. If trees had more than 1 stem at 130 cm, the thickest stem was used. Plots were situated within the forest stands at a distance of at least 20 m from the forest edge to minimize edge effects. A total of 25 pristine and 23 disturbed forest plots were studied. Pristine forest plots were composed of 5 plots of *Polylepis pepei* B.B. Simpson forest, 7 plots of *P. racemosa* Ruiz & Pav. forest, and 13 plots of *P. subsericans* J.F. Macbr. forest. Disturbed forest plots were composed of 8 plots of *Polylepis pepei* forest, 6 plots of *P. racemosa* forest, 3 plots of *P. sericea* Wedd. forest and 6 plots of *P. subsericans* forest.

2.1.3 Grassland structure sampling

Within each 2x2m^2 plot from pristine and disturbed forest and grassland habitats (see '2.2.1 Vegetation sampling' below for more details), the average height of forbs was measured from soil level, with average values being calculated by measuring 10 times in each plot then calculating the mean. Maximum height was calculated of the tallest forb present in the plot. Percentage cover of bare soil and litter was calculated by overlaying a grid on the plot and estimating the cover.

2.2 Biodiversity sampling design

2.2.1 Vegetation sampling

The study was conducted over eight sites; three sites in the Cordillera Vilcabamba and five sites in the Cordillera Urubamba (Fig. S1).

Each of the eight sites were partitioned into four habitat types :

1. Pristine forest
2. Pristine grassland
3. Disturbed forest
4. Disturbed grassland

Forest vegetation refers to plots where canopy cover was >1%. Plots of grassland vegetation were located in open areas at a distance >10 m from the closest tree. At site 1 and 5 the 'disturbed forest' habitat type was not present due to extensive deforestation in the area (Heitkamp et al. 2014; Sylvester et al. 2014) and so plots were made in the other three habitat types.

Within each habitat type for each site, 10–33 plots of 2x2m^2 each were studied for species composition and abiotic variables from representative patches of vegetation. This resulted in a total of 472 2x2m^2 plots (160 pristine forest plots, 83 pristine grassland plots, 118 disturbed forest plots and 111 disturbed grassland plots). Plots were spaced with at least 5 m distance between them, and a maximum distance of 300 m from the nearest plot, to sample as much variability in the vegetation as possible. Voucher specimens were collected and identified in the field or in the herbarium and are deposited at CUZ, LPB, USM, Z. Help in identification was given by specialists: Dr. Nick Hind (Asteraceae), Dr. Ulf Mollau (*Bartsia*), Dr. Zulma Rugulo (*Calamagrostis*), Dr. Xenia Villavicencio (*Calamagrostis*), Juan Carlos Ospina Gonzalez (*Festuca*), Simon Pfanzelt (*Gentianella*), Dr. Michael Sundue (Grammitideae), Dr. Klaus Bernhard von Hagen (*Halenia*), Hibert Huaylla (Iridaceae), Dr. Colin Hughes (*Lupinus*), Dr. Robert Soreng (*Poa*), Dr. Paul Peterson (Poaceae), Dr. Simon Laegaard (Poaceae), Dr. Michael Kessler (Pteridophyta), Dr. Fred Barrie (*Valeriana*).

Environmental variables studied include elevation, soil depth, stoniness of soil, wind exposure, slope inclination and aspect, air temperature, air relative humidity and percentage grazing of plots. Soil depth was measured in different parts of each plot using a metal rod driven into the ground until detained by the first rock and then measured. To compliment this method, sites 1-4 also had soil profiles (3 per habitat type) dug to the C horizon with the length of the whole profile being measured (see 'Soil sampling' below). Stoniness of the soil was semiquantitatively measured based on the soil depth measurements and given a categorical value of 0–100. Wind exposure was given a

categorical value based on the author's opinion of the relative exposure of each plot to wind. Slope inclination was measured using a clinometer with slope exposition being recorded using a compass. The percentage grazing of each plot was recorded by overlaying a grid on the quadrat and estimating the vegetation cover that had been grazed.

Air relative humidity and temperature were recorded at 7 of the 8 sites (sites 1-6 and 8) using digital dataloggers (DS1923 Hygrochron iButtons). Two dataloggers were used per site, one datalogger being placed in the disturbed forest habitat (or placed under bunch grasses if no disturbed forest vegetation was present, i.e. sites 1 and 5) and one in the pristine forest habitat type. Dataloggers were placed on raised platforms 10 cm from the soil surface and were sheltered from direct insolation. They were set to record at 2 hourly intervals over a 12 month period. Recordings were made for at least 12 months per site during the period from October 2010 – August 2013 with certain sites having consecutive dataloggers placed. Daily mean, daily mean minimum and daily mean maximum, and absolute minimum and maximum air temperatures and relative humidity were calculated from the data collected and are presented in table S1.

2.2.2 Forest epiphyte sampling

Pristine *Polylepis* forests of sites 1-4 of the Cordillera Urubamba were studied for *Polylepis* lichen epiphyte diversity and composition using the methodology developed by Gradstein et al. (2003) for surveying epiphytes. This protocol was designed for a rapid and representative analysis of vascular and non-vascular epiphytes in a hectare of forest. The authors recommend sampling 8 trees, with no more than half of the selected trees belonging to the same genus or species. In our case, we have sampled a larger amount than recommended, with (6-)8 trees being studied per site and all trees sampled belonging to the genus *Polylepis* with sites 1 and 3 having *Polylepis subsericans*, and sites 2 and 4 having *Polylepis racemosa*. Both these *Polylepis* species were very similar in terms of general morphology, architecture, bark etc. and so species specific differences were deemed insignificant in affecting lichen diversity meaning that comparisons could be made between forests.

In the pristine forest habitat type of sites 1, 2, and 4, eight trees were studied and, at site 3, six trees were studied, resulting in a total of 30 trees being studied. Trees selected were located within the *Polylepis* forest at a minimum distance of 20 m from the forest edge to minimise edge effects. Trees sampled were spaced with a distance of at least 20 m seperating them so that a better representation of the lichen flora from each site could be sampled. Due to the high proportion of standing deadwood trees and the high diversity and abundance of lichens noted on these trees (Fig. 2F), 4 of the 8 trees studied were standing deadwood of the same species. All trees studied had a similar height (6–7 m) and dbh (c. 20 cm) so that we could control for the effect of tree size on lichen diversity. The basic sampling unit of the study was 20 x 30 cm sections of the tree that exhibit a representative cryptogam diversity of that area of the tree. A total of 216 plots, 16 plots in each living tree and 12 plots in each dead tree were evaluated. To ensure representative sampling and because the *Polylepis* trees studied were small, all epiphytic lichens were collected from three areas of each tree: bole of 0–2 m, the inner canopy and the last 60 cm of branches, with four samples from each cardinal direction being collected for each area (recommended by Gradstein et al. 2003, amendment to

methodology of Normann et al. 2010). The samples were preserved by air drying so that identification of species could be done under the microscope once in the herbarium. Voucher specimens of the lichens can be found in CUZ, B, LPB, Z.

2.3 Soil sampling design

Soil sampling was focused on sites 1-4 of the Cordillera Urubamba. To assure the comparability of pristine and managed habitats within one site, ecosystem forming factors (climate, organisms, relief, parent material, time; Amundson and Jenny 1997) were kept constant. However, relief and parent material differed slightly between sites, which was included into the structure of the statistical model. All sites in the Cordillera Urubamba were located well above the shoulders of the U-shaped valleys, indicating no direct glaciation in the last glacial maximum. Positions of the pits were chosen to avoid major accumulation or erosion processes and were proximate to vegetation plots. Three pits per habitat type (pristine forest, pristine grassland, disturbed forest and disturbed grassland) were chosen in the field. Pits were dug by hand as deep as possible, reaching down to continuous bedrock. After recognising that soils comprised only one, sometimes very thick, A-horizon, sampling was done in depth increments (0-5, 5-10, 10-20, 20-30, 30-40, and >40 cm). Volumetric samples were taken from each layer using the volume replacement method (Maynard and Curran 2008).

Soil mass calculation

Moist field samples were scaled and sieved to 2 mm. The rock and organic residue on the sieve was cleaned with tap water and separated. Roots were dried at 70°C, rocks at 105°C and both were scaled after cooling in a desiccator. Subsamples of the fine earth were dried at 40°C and 105°C (48 hours) for analysis and determination of dry mass (van Reeuwijk 2002). Calculations of the mass of fine earth per square meter were done as follows (Maynard and Curran 2008):

$$\rho_{w,i} = \frac{W_{fe,i} + W_{r,i}}{V_i} \qquad \text{Eq (1)}$$

$$M_{w,i} = \rho_{w,i} \times h_i \qquad \text{Eq (2)}$$

$$M_{fe} = \sum_{i=1}^{n} \frac{M_{w,i} \times 100}{(W_{r,i} / W_{fe,i} \times 100) + 100} \qquad \text{Eq (3)}$$

Where ρ_w is the bulk density of the weathered pedon (i.e., fine earth and rock fragments; g cm^{-3}) of layer *i*, $W_{fe,i}$ is the weight of oven-dry fine earth (g) of layer *i*, $W_{r,i}$ is the weight of rocks (g) in layer *i*, V_i is the total volume (g cm^{-3}) of the undisturbed sample (i.e., the hole in the profile wall) in layer *i*, $M_{w,i}$ is the mass of the weathered pedon (kg m^{-2}) in layer *i*, h_i is the height (mm) of layer *i* and M_{fe} is the mass of fine earth (kg m^{-2}) of the whole profile. The bulk density of fine earth (ρ_{fe}, g cm^{-3}) of layer *i* was calculated as:

$$\rho_{fe,i} = \frac{W_{fe,i}}{V_i - (W_{r,i} / 2.65)} \qquad \text{Eq (4)}$$

Where 2.65 is the assumed density of rocks (g cm^{-3}).

Root biomass

A subsample of soil (20 g) was soaked in demineralised water and poured over a 250 µm sieve (Hertel and Leuschner 2002). Remaining soil particles and roots were divided by swirling and decantation and handpicking with tweezers. Roots were dried (70°C) and scaled and the total biomass was calculated based on the proportion of the subsample compared with the total sample and the soil mass. Since roots were sampled in order to have an estimate of this carbon stock, we made no distinction according to species and did not separate dead from living roots.

Soil analysis

Carbon and nitrogen were measured by dry combustion at 950°C (Truspec CHN LECO, St Joseph, MI, USA). Carbon and nitrogen concentrations were converted to stocks based on the soil mass calculated. Due to the low pH-values, we assumed that total carbon equals soil organic carbon (Vuong et al. 2013). Measurements of pH were done in a slurry with 1:5 (v/v) soil-to-solution (0.1 M $CaCl_2$) ratio (ISO 10390:2005). Effective cation exchange capacity was determined by the extraction procedure of Lüer & Böhmer (2000) in un-buffered solution. Results, therefore, represent the cation exchange capacity of the actual soil pH. Ammonium oxalate extracted poorly ordered forms of Fe and Al oxides (Torrent et al. 1980). After determining Al and Fe concentrations in the extract, we calculated the concentration of short-range-ordered (SRO) minerals as SRO = 0.5Fe + Al (Kramer et al. 2012; WRB 2014). Element concentrations in the extracts were measured by ICP-OES (Optima 4300 DV, Perkin Elmer Instruments, Norwalk, USA).

Isotopic signatures of soil nitrogen (15N) were measured at the Centre for Stable Isotope Research and Analysis, Georg-August-University Göttingen, Germany with an isotope-ratio mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) coupled with an elemental analyser (NA1110, CE-Instruments, Rodano, Italy). Atom % abundance (*A*) is calculated as

$$A = 100\left(\frac{R_{sample}}{R_{sample}+1}\right) \qquad \text{Eq (5)}$$

Where R_{sample} is the ^{15}N:^{14}N isotope ratio. Because the ^{15}N abundance is relatively small (R of atmospheric N_2 is 0.0036765 (Robinson 2001), slight enrichments in samples are more conveniently reported against a standard (atmospheric N_2, R_{air}), which is expressed as $\delta^{15}N$ (‰ air):

$$\delta^{15}N = 1000\left(\frac{R_{sample}-R_{air}}{R_{air}}\right) \qquad \text{Eq (6)}$$

Natural abundance of 15N in soils is a powerful integrated indicator for processes of the nitrogen cycle in soils (Høgberg 1997; Robinson 2001). Enrichment of 15N is generally a consequence of microbial fractionation against heavier isotopes leading to selective enrichment of 15N over 14N in soil. Subsequent gaseous and leaching losses lead to depletion of 14N in ecosystems. However, when processes should be derived directly, the

signature of all important ecosystem N-pools have to be known. Therefore the $\delta^{15}N$ signature serves here as a general and integrated indicator for N-cycling.

3. Data analysis and discussion

For all comparisons between habitat types, unless specified otherwise, mixed effects models were used with the fixed effects being 'human impact, with the two levels 'Pristine' and 'Disturbed', 'vegetation type', with the two levels 'Forest' and 'Grassland', and the interaction between 'accessibility' and 'vegetation type'. The factor 'site', with eight levels corresponding to the eight sites studied, was treated as a random effect. Model selection followed the protocol advocated by Bolker et al. (2009). Linear mixed effects models (LMM's), fit using restricted maximum likelihood estimation (REML) t-tests using Satterthwaite approximations to degrees of freedom, were used where the data was normally distributed with homogeneity of variance, or could be successfully transformed to achieve this. For data that could not be successfully transformed, we used generalised linear mixed effects models (GLMM's) with Laplace approximation. This is seen to be more accurate than Penalised QuasiLikelihood (PQL) approximation, with reduced bias and the ability to approximate the true GLMM likelihood, rather than a quasi-likelihood (Raudenbush et al. 2000; Bolker et al. 2009). Laplace approximation is also considered to work better where the mean number in samples is <5 (Bolker et al. 2009) and, as this was the case in certain analyses, this method was preferred over PQL approximation. All GLMM's were fitted in the R package 'glmmadmb' version 0.8.0 and LMM's were fitted using R package 'lmerTest' version 1.0. Proportional and percentage cover data were logit transformed, as opposed to arcsine square root transformed, on grounds of interpretability and because arcsine transformation can produce nonsensical predictions (Warton & Hui 2011).

Data was checked for normality using the Shapiro-Wilk normality test and, when non-normal data could be successfully transformed, transformation was done following Webster (2001). Homogeneity of variance was checked using the Bartlett test and, when non-normally distributed, the Levene (Fox 2008) and Fligner-Killeen tests were used. All analyses were performed in R 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria).

3.1 Comparability of site conditions (Table S20)

To test whether there were differences in climate between the pristine and disturbed habitat types we, firstly, calculated 13 climate properties from the temperature and relative humidity data collected and then, after successful transformation of certain climate parameters (for details on each parameter and the type of transformation for each parameter see Table S20), subjected this data to LMM's (Table S20). The fixed effect was 'human impact', with two levels 'Pristine' and 'Disturbed'. The factor 'site', with seven levels corresponding to the sites 1 – 6 and 8, and the covariate 'elevation' were treated as random effects. A total of 19 data sources were used; 9 from pristine habitats and 10 from disturbed habitats across the seven sites. Quantitatively similar results were obtained when running Gaussian GLMM's as well as non-parametric Kruskal-Wallis tests and so only the LMM results are shown here. No significant differences were found between pristine and disturbed sites for any of the climate variables and so we can

discount climate as a possible influencing factor on the differences in vegetation and soils seen between the disturbed and pristine habitat types.

3.2 Vegetation structure analyses

3.2.1 Calculating potential forest-grassland distributions (Fig. 1B; Table S2, S3, S18)

We predicted the potential carbon stocks of the Cordillera Urubamba by extrapolating the proportions of forest and grassland in pristine areas (i.e. 70.33% and 29.67%, respectively; Table S2, S3) to all areas of the Cordillera above 4200 m.a.s.l. that were found to host zonal vegetation. This resulted that the Cordillera Urubamba could hold 54,075.196 km^2 of forest and 22,814.502 km^2 of grassland (Table S18). Here we implicitly assume that the pristine sites studied are representative of the entire variability in the landscape. Zonal vegetation comprising both forest and grassland was found to ca. 4900 m, with all areas above 4900 m found to be azonal, usually rocky or glaciated, terrain. As forest was found at the elevational limit of zonal vegetation, albeit in smaller amounts (0.4 km^2 between 4850 – 4900 m.a.s.l.) compared to grassland (13.9 km^2 between 4850 – 4900 m.a.s.l.), this implies that forest distribution can potentially extend across the entire elevational range of zonal vegetation.

Because the majority of pristine areas had a West or South-West aspect, it was difficult to test whether topography (i.e. elevation and aspect) had an effect on pristine forest distribution, and whether this should be included when modelling potential forest distribution. Certain research has found topography to be an important determinant of *Polylepis* forest distribution (Bader & Ruitgen 2008; Gosling et al. 2009), but this research failed to isolate the effect of human disturbance. Therefore, it remains unclear how natural forest distribution is determined by topography. This highlights some shortcomings in our approach for calculating potential forest distributions, as the pristine vegetation studied does not include all the landscape variability and, thus, our results are likely to be biased.

3.2.2 Forest structure comparisons (Fig. 1C,D; Table S4, S5)

Stand basal area was calculated for each forest plot by, firstly, converting dbh (diameter at breast height; 130 cm) to tree basal area for every tree present in each 10 x 10 m forest plot using the equation:

$$BA = \frac{\pi \times (DBH/2)^2}{144} \qquad \text{Eq (7)}$$

These values of tree basal area were then summed up for each plot and divided by the area of land in which they were measured (i.e. 10 x 10 m) to give the stand basal area in m^2/ha for each plot.

Aboveground biomass of each tree was calculated using the allometric equation of Vasquez et al. (2014). The allometric equation proposed by Fehse et al. (2002) could not be used as we had not recorded data on 'form factor'. To allow our data to be fitted to the allometric equation proposed by Vasquez et al. (2014), who measure tree diameter at 50 cm from the ground, we created a linear model to extrapolate dbh (130cm from ground) data to that from 50cm from the ground. To do this, 15 trees of *Polylepis racemosa* and 15 trees of *Polylepis incana* Kunth of different sizes were measured at 130

cm and 50 cm from ground level. These trees were growing in the vicinity of Cusco. If the trees had more than 1 stem at 130 cm, the thickest stem was used, as was also done in the forest plot sampling. The values of dbh (130 cm) and tree bole diameter at 50 cm were then subjected to a linear regression (Fig. S3) to retrieve a linear model which was used to convert dbh values to bole diameter at 50 cm. The equation used to predict bole diameter at 50cm had reasonable accuracy ($R^2 = 0.77$; Fig. S3).

Diameter at breast height (dbh) values were converted to those of diameter at 50 cm height using the equation:

$$\text{Diameter of bole at 50cm} = 1.1613 \times DBH + 0.4628 \quad \text{(Eq 8)}$$

These values, as well as tree height values, were then submitted to the allometric equation of Vasquez et al. (2014) in order to calculate total biomass for each individual tree:

$$\text{Biomass} = -16.51 + 40.26 \times \text{tree height (log10)} + 9.30 \times \text{tree diameter (log10)} \quad \text{(Eq 9)}$$

Following this, total biomass and average biomass of trees per 10 x 10 m forest plot was calculated. Biomass values were converted to carbon assuming a 50 % carbon content in aboveground biomass (Giese et al. 2003; Schlesinger and Bernard 2013).

Values of total, mean and maximum aboveground biomass per 10x10 m plot, stand basal area, mean dbh, mean and maximum tree height per 10x10 m plot were then compared between pristine and disturbed forests using LMM's with certain values needing log transformation to reach normality. 'Human impact' (factor with two levels; 'Pristine' and 'Disturbed') was treated as a fixed effect, whilst 'elevation', 'tree species' (i.e. whether forests were dominated by *P. pepei*, *P. racemosa. P. sericea* or *P. subsericans*) and 'Cordillera' (i.e. Cordillera Urubamba or Cordillera Vilcabamba) were treated as random effects. *Polylepis* forests in the Cordillera Urubamba and Vilcabamba contain a single species of *Polylepis* and, often, another *Gynoxys* (Asteraceae) species per forest. To ensure no bias based on species specific effects on forest density when comparing pristine and disturbed forest properties, we treated 'tree species' and 'Cordillera' as random effects in the GLMM.

Comparison of the proportion of trees that were standing deadwood per 10x10 m plot was done by, first, logit transforming that values and then fitting the data to a Gaussian GLMM with zero inflation being taken into account. Human impact was treated as the fixed effect and 'elevation', 'Cordillera' and 'species specific forest type' as random effects. To treat elevation as a random effect, elevational values 4211 – 4812 m.a.s.l. were converted into a factor with 20 levels with each level referring to an elevational difference of 30.05 m.

3.2.3 Herbaceous community structure (Fig. 1E, S5; Table S4)

Differences in average and maximum height of forb communities between the four habitat types were compared using gamma GLMM's with a log link function. Differences in cover of bare soil and litter were compared using Gaussian GLMM's after logit transformation, with zero inflation being taken into account when analysing bare soil. LMM's and Kruskall-Wallis non-parametric tests gave qualitatively similar results so only the GLMM results are shown here.

3.3 Biodiversity analyses

Nomenclature of vascular plants follows that of Tropicos.org (2015). Nomenclature of lichens follows that of Index Fungorum (2015).

3.3.1 Species richness comparisons (Fig. 2A, S6A; Table S6)

A total of 334 vascular plant species were recorded from all plots. To compare number of species of vascular plant per $2x2m^2$ plot in the different habitat types, plot data was subjected to a negative binomial GLMM with a log link function to account for the heterogeneity of variance.

3.3.2 Beta diversity comparisons (Fig. 2B; Table S7)

We chose to calculate beta diversity by comparing differences between habitat types at a site-level, as opposed to plot-level, basis because we were interested in geographic turnover of habitats between sites. This yielded a total sample size of 30 (sites 1 and 5 lacked the habitat type 'disturbed forest').

We calculated pairwise site-habitat type Sørensen dissimilarities for vascular plant species using the function vegdist in R package 'vegan' version 2.2-0. This yielded a total Sørensen dissimilarities sample size of 112 (28 for each category). We then compared differences in Sørensen dissimilarities of the four habitat types via two way ANOVA with interaction followed by Tukey test. The fixed effects in the model were human impact (with levels 'disturbed' and 'pristine') and vegetation (with levels 'forest' and 'grassland') and the interaction between these factors.

3.3.3 Comparisons of undescribed species per habitat type (Fig. 2C, S6A; Table S6, S8, S9, S10)

Species were deemed to be undescribed, new species to science after thorough literature searching and consultation with specialists: Dr. Nick Hind (Asteraceae), Dr. Robert Soreng (*Poa*), Dr. Zulma Rugulo (*Calamagrostis*), Dr. Xenia Villavicencio (*Calamagrostis*), Dr. Ulf Mollau (*Bartsia*), Dr. Simon Laegaard (Poaceae), Hibert Huaylla (*Cardenanthus*), Simon Pfanzelt (*Gentianella*), Dr. Fred Barrie (*Valeriana*), Dr. Michael Sundue (*Moranopteris*). A list of the 15 undescribed, new species to science can be found in Table S8. After logit transformation, cover and proportion of undescribed species per plot were compared between the four habitat types using Gaussian GLMM's with zero-inflation being accounted for.

3.3.4 Comparisons of introduced species per habitat type (Fig. 2D, S6B; Table S6, S9, S10)

Species were deemed 'introduced' or 'alien' if they were found outside of their native distributional range, having arrived there by human activity, either deliberate or accidental. After logit transformation, cover and proportion of introduced species per plot were compared between the four habitat types using Gaussian GLMM's with zero-inflation being accounted for. The introduced species are highlighted in blue in Table S10.

3.3.5 Vascular plant indicator species analyses (Table S8, S9, S10)
To identify the species characteristic of each habitat type, and to evaluate the proportion of these indicator species that were undescribed or introduced, Indicator Species Analyses were performed using the Indval method (Dufrêne & Legendre 1997). We compared and contrasted the four habitat types: Pristine forest, Pristine grassland, Disturbed forest, Disturbed grassland (Table S9). Analysis was done using the R package 'labdsv' version 1.5-0.

3.3.6 Species range size comparisons (Fig. 2E; Table S6)
Of the 334 vascular plant species encountered, all but 10 could not be reliably identified to species-level and their data was omitted from this analysis. Latitudinal range size was considered a good proxy for overall range size as the majority of widespread species were distributed throughout the length of the Andes. This approach has been employed in other studies of Andean vegetation (Kessler 2001, 2002; Lozada et al. 2008) and has proved to be an effective objective way of comparing range size.

The latitudinal distribution data of all species were extracted from the W^3 TROPICOS of the Missouri Botanical Garden's VAST nomenclatural database and associated authority files (http://www.tropicos.org/). Latitudinal range size for each species was measured as the latitudinal difference between the northern- and the southern-most specimen record. Where no specimen records were available, information on distribution from references provided in W^3 TROPICOS would be used. W^3 TROPICOS data was chosen as it was considered more reliable than data from the Global Biodiversity Information Facility (GBIF; www.gbif.org), with there being more likelihood that taxonomic specialists have checked the specimens for correct determination. Values were recorded at the grain size of latitudinal minutes. To be conservative, when distribution data by country were used, the latitudinal limit was taken from the most southern or most northern alpine area of that country. We compared average latitudinal range size of vascular plant species per plot between the four habitat types using a gamma GLMM with log link function.

3.3.7 Plant trait comparisons (Fig. 2G, S7, S8; Table S12, S13)
To see how plant form differed between the pristine and disturbed habitat types, we scored each species according to their life form and grazing-related morphological traits with the methodology modified from Diaz et al. (1992) and Miehe et al. (2011). The 32 traits scored can be found in Table S13.

Species lifeform was categorised based on Raunkiær's (1974) lifeform classification. As the majority of tree species measured between 3–12 m, we combined the classes Mesophanerophyte and Microphanerophyte. Arboreal vascular hemiparasite *Tristerix longebracteatus* was included in the epiphyte category whilst grassland vascular hemiparasites in the genera *Bartsia*, *Calceolaria* and *Castilleja* were classed as hemicryptophytes. This was done because the hemiparasitic lifeform was not seen to have much value in interpreting differences in vegetation based on anthropogenic impact.

Trait data was subjected to PCA from which 8 scaled principal components that represented 71.0% of the variation in the data were extracted for each species. Each principal component related to different morphologies and/or strategies to cope with grazing/burning and are summarised in Table S13. These principal component values

were then scored per species for each 2x2m^2 plot and mean values were calculated per plot. The mean values per plot of each principal component were then compared between the four habitat types using Gaussian GLMM's with identity link function (Table S12).

3.3.8 Lichen epiphyte diversity and composition comparisons (Fig. 2F; Table S6, S11)
After observing high lichen diversity and abundance in standing deadwood trees from pristine forests, which were absent from disturbed forests due to firewood extraction by local people, it was decided that this should be studied. Lichen diversity in pristine and disturbed forests can be indirectly compared based on first comparing diversity and composition of lichens in living and deadwood trees from pristine forests and then comparing data on forest structure for pristine and disturbed forests to show that disturbed forests lack standing deadwood trees and, thus, have a lower overall lichen diversity. Species richness was compared between dead and live trees by grouping all plots into substrate type 'deadwood' (N= 228) or 'live' (N=179) and subjecting these to negative binomial GLMM's with log link function to account for the heterogeneity of variance (Table S6). The fixed effect was 'substrate type', with the two levels 'Deadwood' and 'Live', whilst the factor 'site', with four levels corresponding to the sites 1 – 4 of the Cordillera Urubamba, was treated as a random effect.

Indicator Species Analyses were performed using the Indval method (Dufrêne & Legendre 1997) to compare and contrast the two habitat types: Deadwood and Live Tree (Table S11). Species that were considered to be important components of each habitat type were given larger indval values and those which were seen to be more restricted to a certain habitat type were given higher significance values for that habitat type. 28 species were retrieved as significant ($p<0.05$) indicators for the deadwood habitat whilst no species were retrieved as significant for live trees (Table S11).

3.4 Soil analyses (Fig. 3, S9; Table S14, S15)
After successful transformation of certain soil parameters (for the type of transformation for each parameter see Table S15), all were subjected to linear mixed effects models using restricted maximum likelihood estimation (REML). Quantitatively similar results were obtained when running Gaussian GLMM with Laplace approximation as well as non-parametric Kruskal-Wallis tests and so only the LMM results are shown here. The fixed effects were 'human impact, with the two levels 'Pristine' and 'Disturbed', 'vegetation type', with the two levels 'Forest' and 'Grassland', and the interaction between 'accessibility' and 'vegetation type'. The factor 'site', with four levels corresponding to the sites 1 – 4 studied from the Cordillera Urubamba, was treated as a random effect. Absolute pH values were not used, but, instead, we used the actual proton (H+) concentration as this is metric and rationally scaled.

3.5 Quantification of carbon stocks (Fig. 4, S10; Table S16, S17, S18, S19)
We predicted the potential carbon stocks of the Cordillera Urubamba using the data on potential forest and grassland distribution calculated in section 3.2.1 above (i.e. the Cordillera Urubamba could hold 54,075.196 km^2 of forest and 22,814.502 km^2 of grassland). We then extrapolated the values (min., max. lower and upper quartile and mean) per m^2 of Soil Organic carbon (SOC), aboveground tree carbon and root carbon collected from pristine forest and grassland habitats (Table S16) across the entire

Cordillera to give us the potential carbon stocks (Table S18, S19). Following this, we employed the same methodology to calculate actual carbon stocks by extrapolating the values (min., max. lower and upper quartile and mean) per m^2 of the carbon stocks to the quantity of land occupied by pristine and disturbed forest and grassland that was calculated in the landscape mapping approach (Table S2). It is likely that estimates could be a lot higher as we did not investigate soil inorganic carbon, which has been shown as an important carbon stock in high mountain ecosystems (Yang et al. 2010), or aboveground herbaceous biomass, although this has a comparatively insignificant carbon stock (Oliveras et al. 2014; Vasquez et al. 2014).

Supplementary Text

1. Vegetation structure

Forest structure

The Cordillera Urubamba had forests that were dominated by either *Polylepis racemosa* or *P. subsericans*, and with *Gynoxys nitida* Muschl. often occurring as a shrub in pristine plots. The Cordillera Vilcabamba had forests that were dominated by *Polylepis pepei*, with pristine plots also having large trees of *Gynoxys cuzcoensis* Cuatrec. as an important component of forest structure.

2. Biodiversity

Vascular plant indicator species analyses (Table S9, S10)

The differences in total number of indicator species (Table S9) retrieved from indval analysis is most likely related to the differences in the alpha diversity between the habitat types (Fig. 2A). When comparing the four habitat types (Table S9), pristine forest was found to contain the greatest proportion of significant ($P<0.05$) indicator species that were new to science (e.g. Sylvester 2014). Six of the 24 species retrieved as being significant indicators were undescribed whilst the disturbed habitats, although having more indicator species, had a much lower proportion of new species. Four other undescribed species were also associated with pristine habitats but were not significant in the analysis (Table S8, S10). Disturbed forest was found to have a high proportion of introduced species (Table S9). Most of the introduced indicator species for disturbed forests were short-lived annuals or biennials (eg. *Poa annua* L., *Capsella bursa-pastoris* (L.) Medik., *Cerastium glomeratum* Thuill., *Veronica arvensis* L. *Stellaria media* (L.) Vill.) with *Ranunculus repens* L. being the only perennial. This may relate to how the high levels of disturbance by cattle in this habitat allow these species to proliferate. Five other introduced species were also associated with disturbed habitats but were not significant in the analysis (Table S10).

Plant trait comparisons (Fig. 2G, S7, S8; Table S12, S13)

Three of the principal components (Principal components 1, 6 and 7) were considered to summarise grazing induced trait syndromes being positively correlated with human impact. PC1 explained 16.3% of the data and refers to the trait syndrome of having a low-growing habit with the stems and flowers being kept close to the soil surface and is a strategy to avoid herbivory. PC6, which summarises the trait syndrome for plants that are not large biennial herbs, explained 7% of the data and refers to a few common species (*Gentianella scarlatiflora* (Gilg) J.S. Pringle, *Cerastium subspicatum* Wedd.) found only in pristine habitats. PC7 explains 5.6% of the variation in the data and represents the trait syndrome of small (5–15 cm) graminoids, that are not spiny, stinging, rosette- or cushion-forming.

Four of the principal components (Principal components 2, 3, 5, and 8) were considered trait syndromes correlated with grazing-absence, being negatively correlated with human impact. PC2 explained 11.7% of the variation in the data and refers to tussock grasses. PC3 explained 9.6% of the variation in the data and referred to large phanerophytes, i.e. trees. PC5 explained 7.4% of the variation in the data and referred to large forbs, often chamaephytes, that had a creeping or stoloniferous habit. PC8 explained

4.8% of the variation in the data and referred to plants that were not spiny, stinging or cushion forming.

PC4 was not found to be correlated with human impact, as there was no significant difference between the representation of this trait syndrome between pristine and disturbed vegetation (Fig. S7, S8). Vegetation type was, however, found to have a significant influence, with forests having a greater representation of this trait syndrome. PC4 explained 8.7% of the data and refers to geophytes that are generally large and not sclerophyllous.

3. Soil

Soil bulk density (Fig. S9; Table S16)

Soil depth ranged from 15 to 90 cm with the median between 40 and 60 cm (Fig. S9) without significant differences between habitats. Bulk density showed surprisingly high values in grazed forests. This may be explained by the tendency of livestock to rest under the shelter of the canopy. Compaction was not obvious in disturbed grassland for the whole profile, but bulk density was higher in the top 10 to 20 cm. Overall the mass of fine soil did not differ between habitats, indicating that erosion was not higher in grazed habitats, as one might expect. Most frequently, anthropogenic pressure on steep land induces erosion with an estimated global value of 50–200 Pg of soil being lost each year (Govers et al. 2014). Nevertheless, the high livestock densities at the study sites did not lead to any obvious signs of erosion, indicating a highly sustainable land use. This may be explained by how, in the entire region, paths of livestock cover the slopes (Fig. 1A), which serve as small terraces breaking the high relief energy. Another possible explanation for why soils were not heavily eroded may relate to how high contents of organic matter protect soils against erosion (Fig. 4C).

Root biomass (Fig 4B; Table S16, S17)

Our root biomass estimates are much higher than those of Oliveras et al. (2014; 0.6 kg m^{-2} for puna grassland at 3500m) and Hertel and Wesche (2008; 0.2 kg m^{-2} for *Polylepis* woodland at 4000m). These studies, however, reported sampling depth of 30 and 2 cm mineral soil, respectively. Taking these differences in sampling depth into account, our data fit quiet well.

Soil classification (Table S14)

Classification of soils followed the IUSS Working Group WRB (2014). All soils were characterised by having a thick A-horizon, overlying continuous rock. The most shallow profiles were located at site 1 and were only 15 cm (pristine grassland) and 20 cm (pristine forest) deep. These soils were classified as Leptosols. They had a mollic horizon (≥ 0.6% soil organic carbon, Munsell colour and chroma ≤ 3, ≥ 0.6% more organic carbon than parent material, a base saturation ≥ 50% and ≥ 10 cm thickness overlying continuous rock) and were classified as Mollic Leptosols. All other soils were deeper than 25 cm and had less than 80% (by volume) rocks. All soils fulfilled the criteria of colour and carbon concentration to be classified as either Phaeozeme or Umbrisol, the difference being the low (> 50%) base saturation in Umbrisols.

Fig. S1

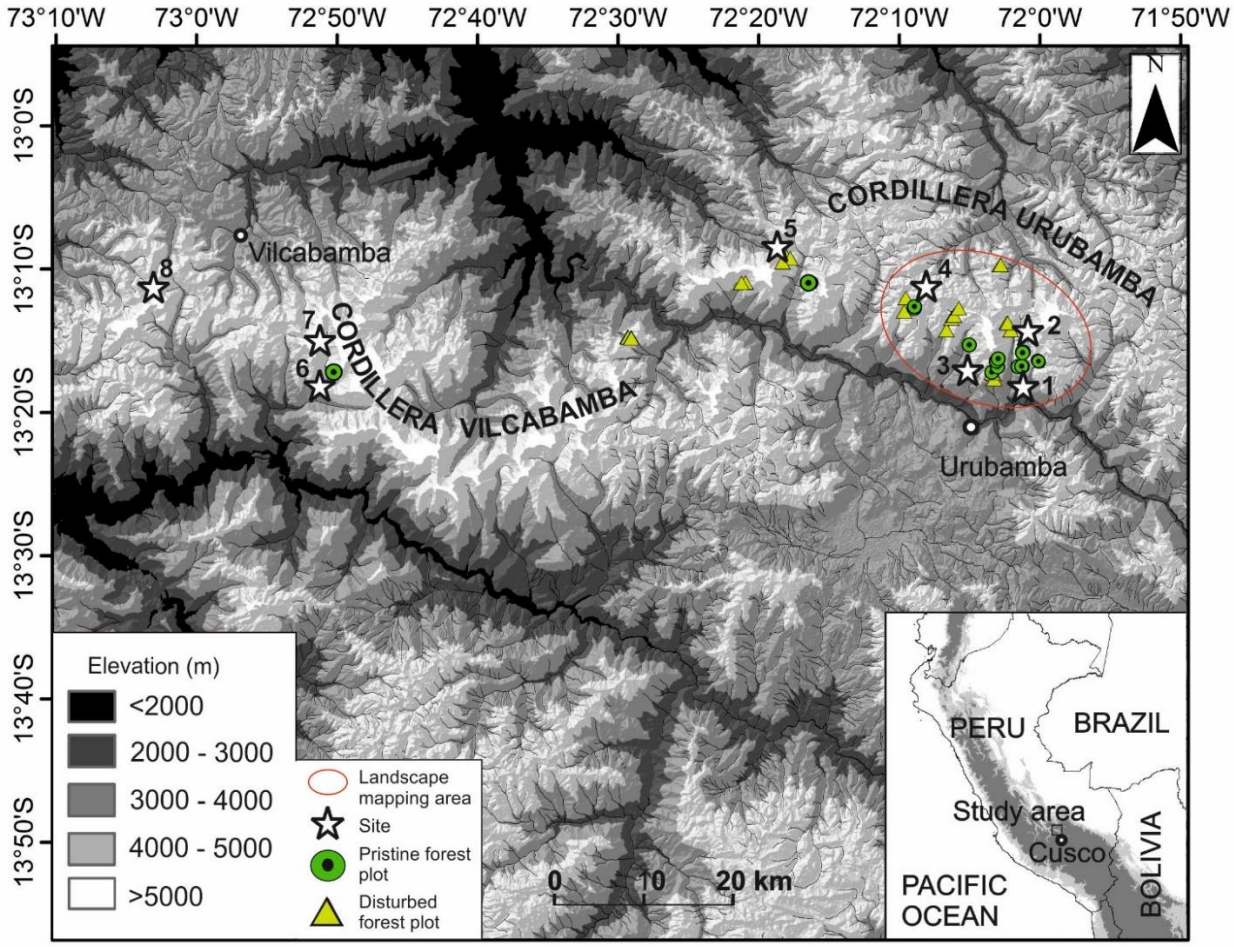

Fig. S1. Map of the study area showing the eight study sites (denoted by numbered stars), the locations of pristine and disturbed forest plots (denoted by green-filled circles and yellow-filled triangles, respectively), and the area used for landscape mapping of woodland and grassland in accessible and inaccessible areas (denoted by a red oval). ASTER DEM raster map provided by METI and NASA Land Processes Distributed Active Archive Center.

Fig. S2

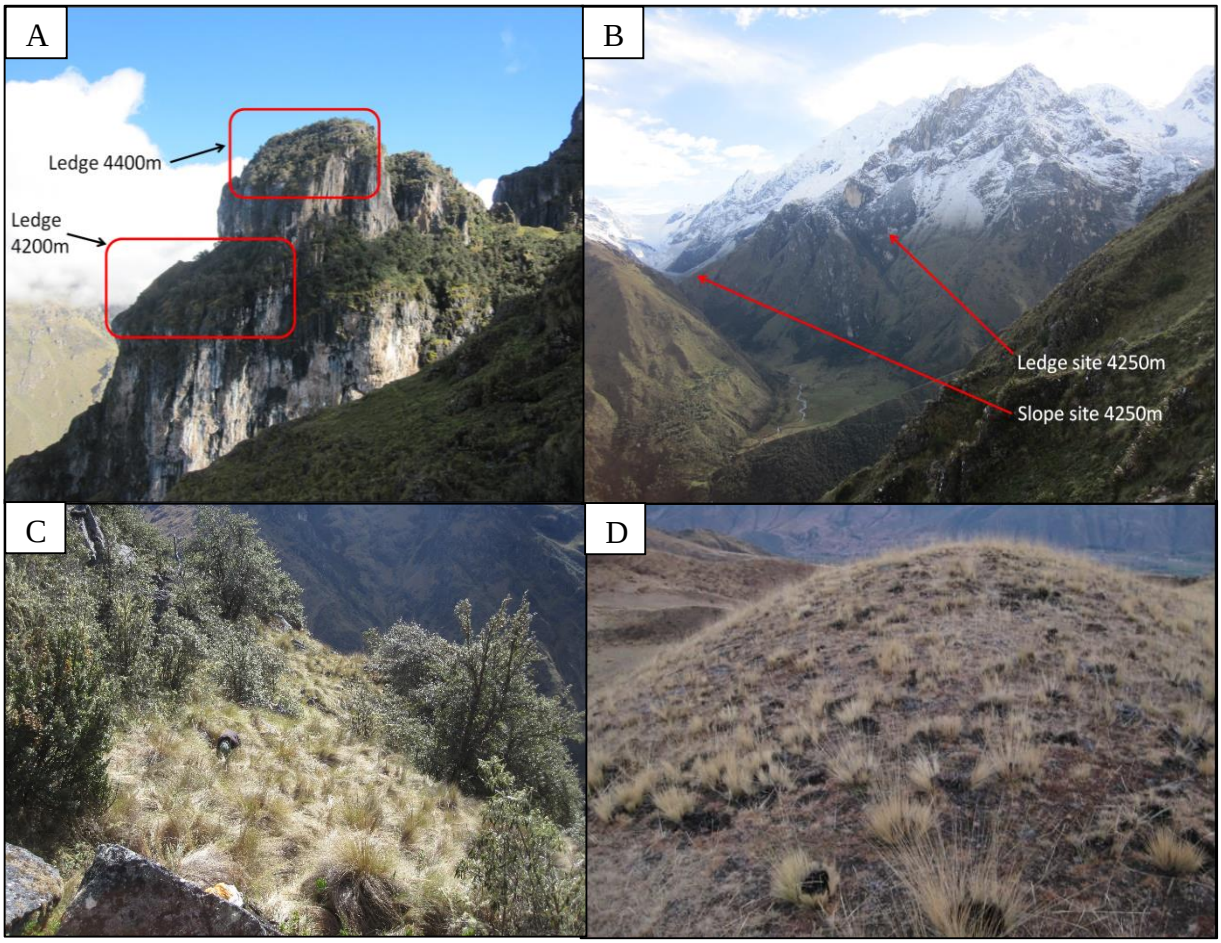

Fig. S2. Impression of the study sites. (A) Example of a study site showing the pristine ledge sites accessed; (B) Example of a study site showing both the pristine ledge and disturbed slope areas studied; (C) Example of pristine vegetation showing a forest grassland mosaic dominated by *Polylepis subsericans* trees and the undescribed tussock grasses, *Deyeuxia* sp. nov. 1 and *Festuca linigluma* sp. nov.; (D) Example of disturbed vegetation showing the dominance of short forbs as well as burnt tussocks. Photographs taken by S.P. Sylvester.

Fig. S3

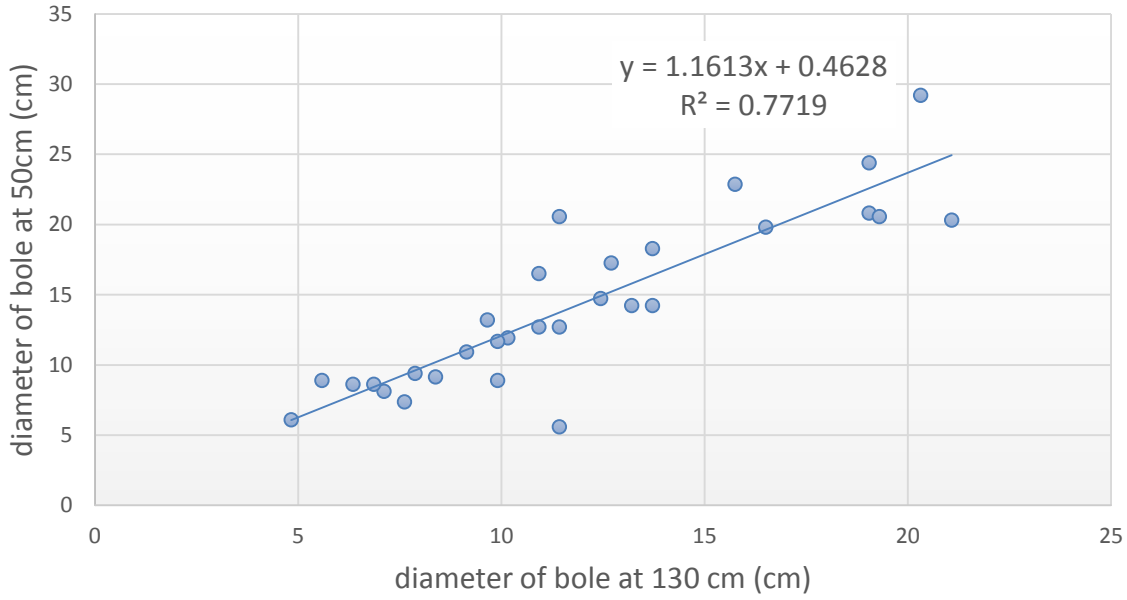

Fig. S3. Tree bole diameters at 50 and 130 cm plotted against each other and used to generate the linear model for predicting tree bole diameter at 50cm using dbh values.

Fig. S4

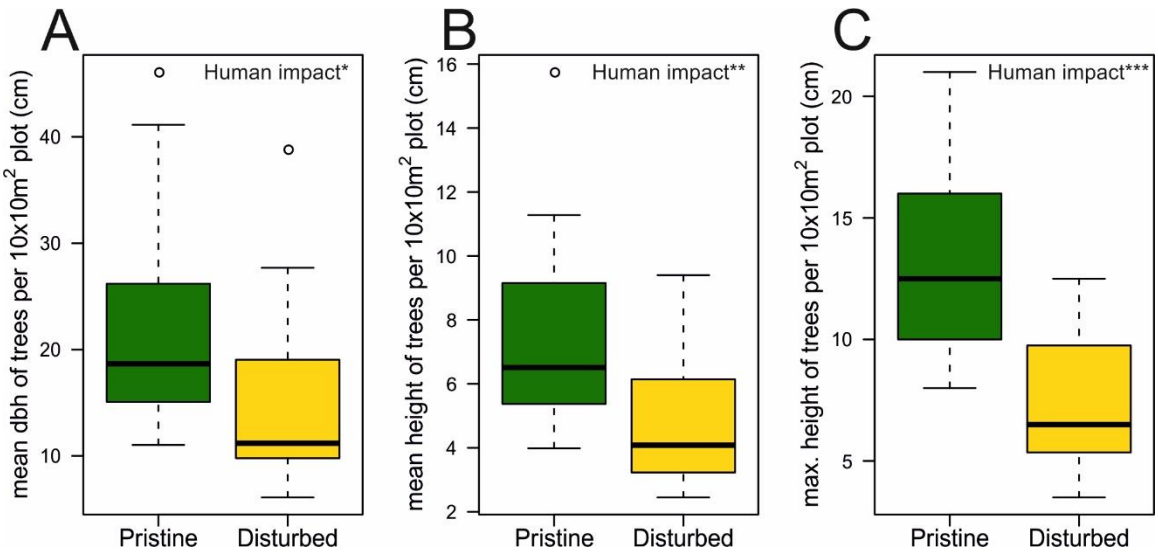

Fig. S4. Differences in mean dbh (A), and mean (B) and maximum height (C) of trees per forest plot between disturbed and pristine *Polylepis* forests. Significant relationships between the structural properties and human impact, found upon analysis using linear mixed models, are noted within the plots (***=p<0.001, **=p<0.01, *=p<0.05). Sample size: Pristine 25, Disturbed 23.

Fig. S5

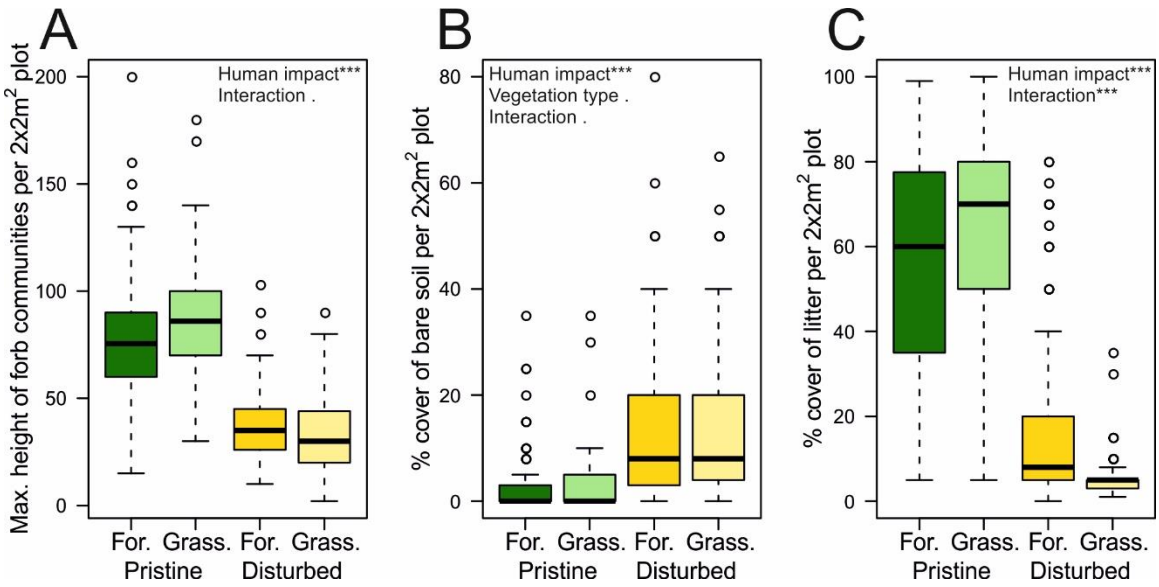

Fig. S5. Differences in herbaceous vegetation structure between the habitat types pristine forest and grassland, and disturbed forest and grassland in terms of maximum height of vegetation (A), cover of bare soil (B), and cover of litter (C) per plot. Significant relationships between the structural properties and fixed effects, found upon analysis using GLMM's, are noted within the plots (***=p<0.001, . =p<0.1). Sample size: Pristine forest 160, Pristine grassland 83, Disturbed forest 118, Disturbed grassland 111.

Fig. S6

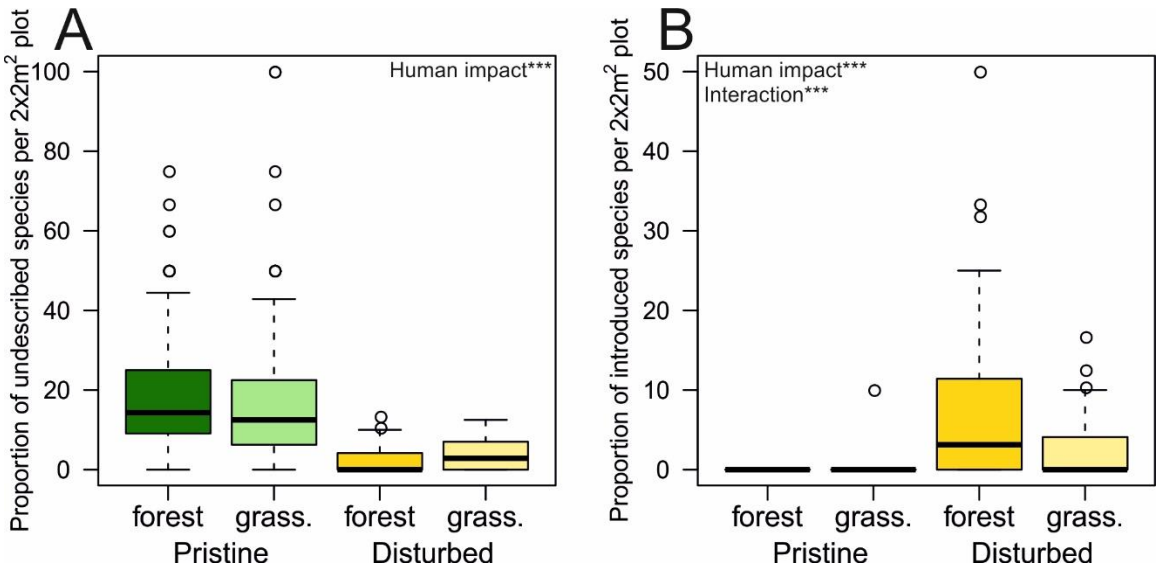

Fig. S6. Proportion of undescribed species (A) and introduced species (B) per plot for the four habitat types: Pristine forest and grassland, disturbed forest and grassland. Significant relationships between the structural properties and fixed effects, found upon analysis using GLMM's, are noted within the plots (***=p<0.001). Sample size: Pristine forest 160, Pristine grassland 83, Disturbed forest 118, Disturbed grassland 111.

Fig. S7

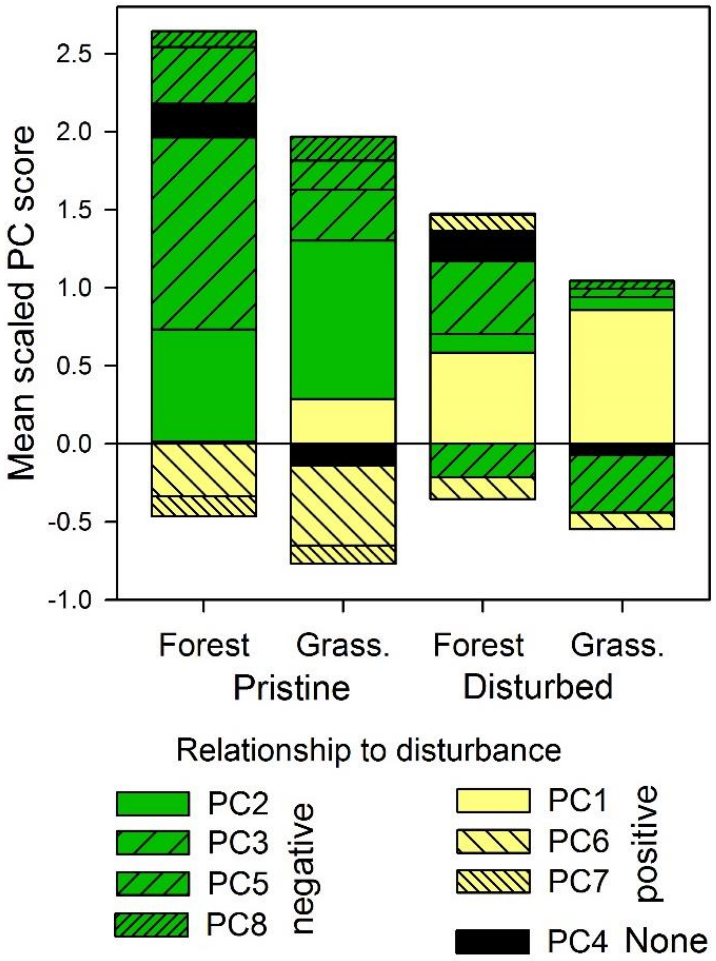

Fig. S7. Comparison of the means of the 8 scaled principal components, referring to plant trait syndromes (Table S13), averaged over all species per 2x2m^2 plot, with their relationship to disturbance shown by the colouring green (negative) and light yellow (positive). Sample size: Pristine forest 160, Pristine grassland 83, Disturbed forest 118, Disturbed grassland 111.

Fig. S8

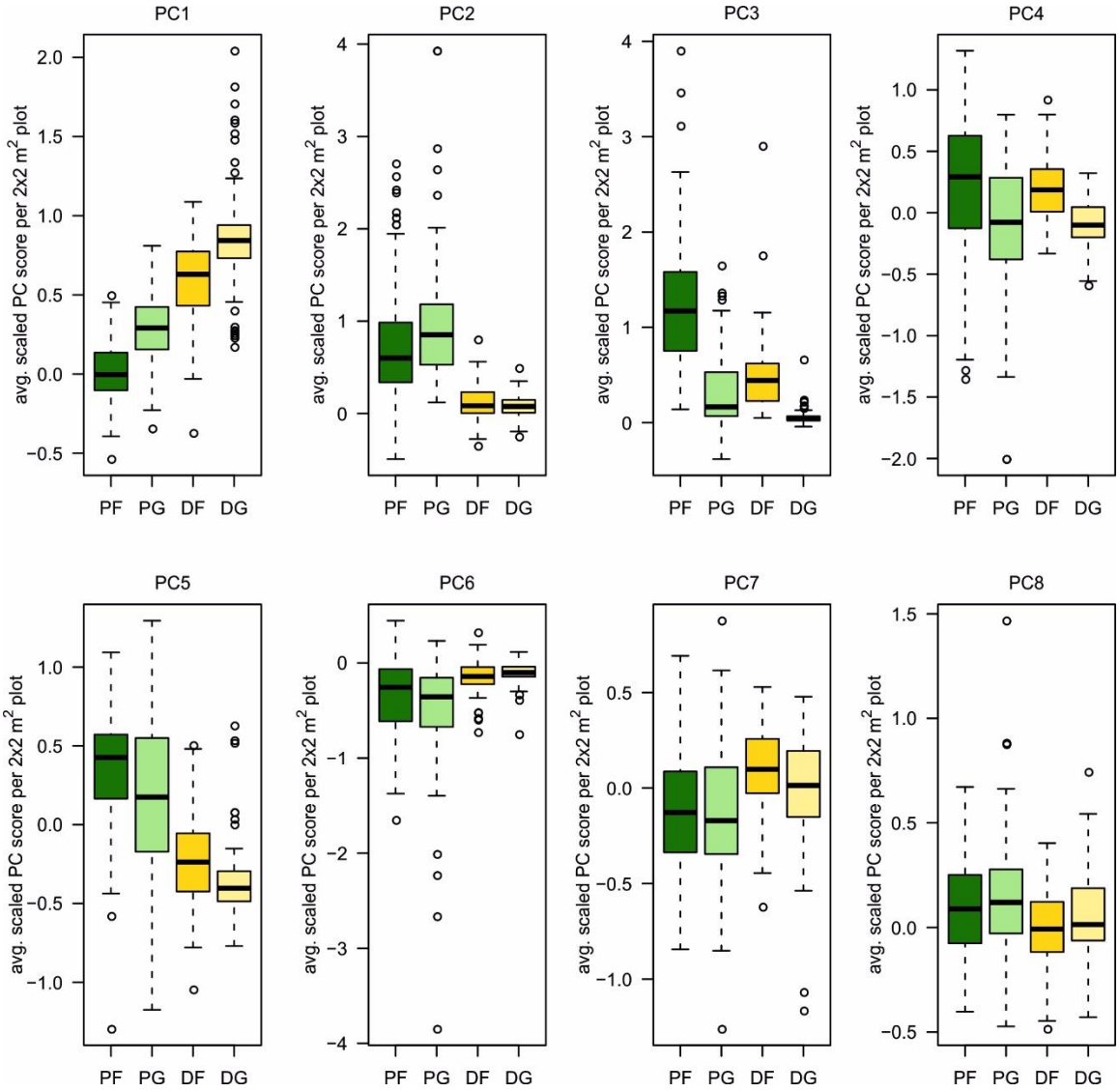

Fig. S8. Differences in mean scaled principal component scores per plot of principal components 1-8 between the habitat types: PF=Pristine Forest, PG=Pristine Grassland, DF=Disturbed Forest, DG=Disturbed Grassland. Significance values of LMM tests can be found in Table S12. Sample size: PF=160, PG=83, DF=118, DG=111.

Fig. S9

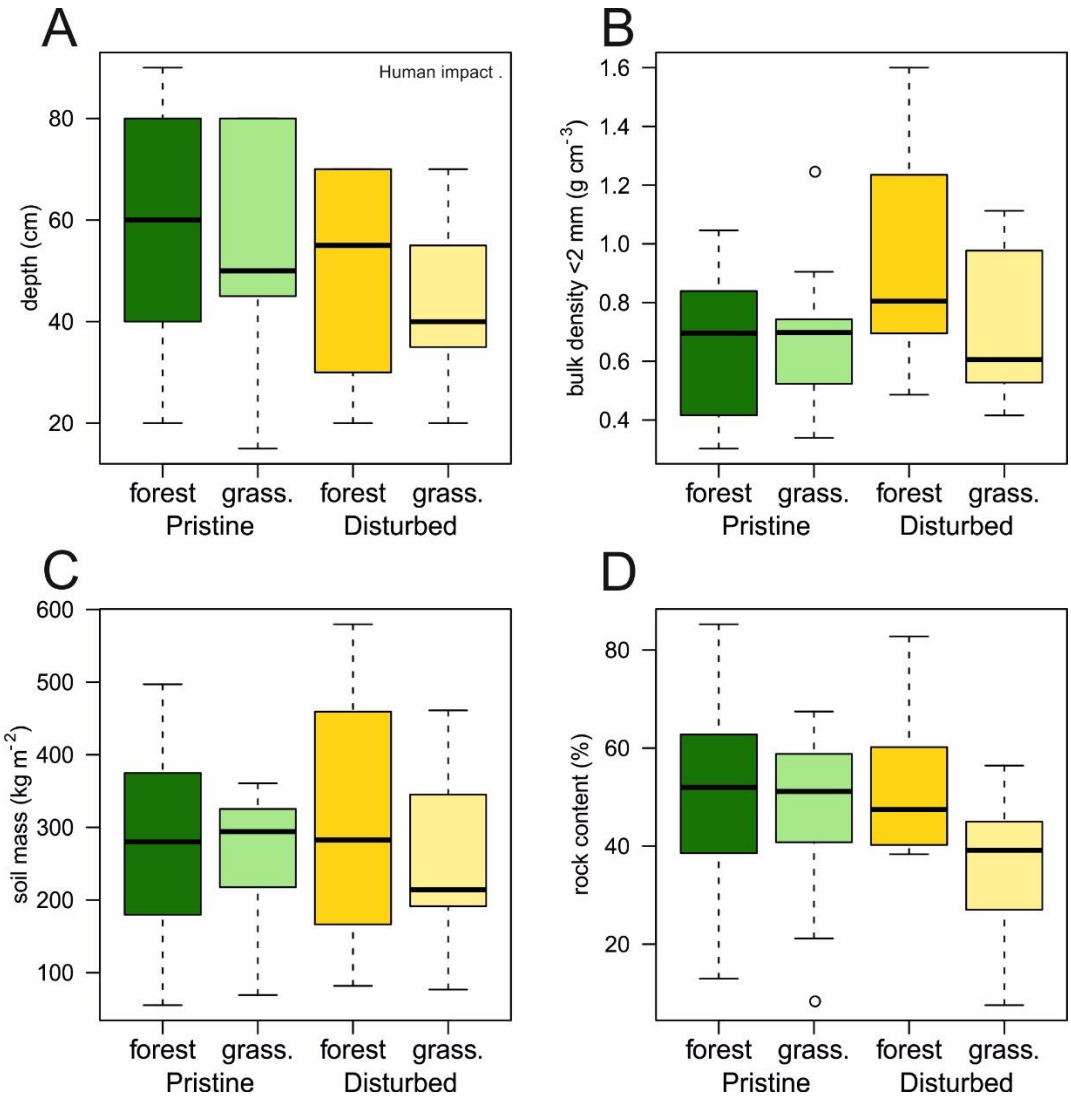

Fig. S9. Differences in depth (A), bulk density (B), mass (C) and rock content (D) of soils between the habitat types pristine forest and grassland, and disturbed forest and grassland. Significant relationships between the structural properties and fixed effects, found upon analysis using LMM's, are noted within the plots (. =p<0.1). Sample size (number of soil profiles): Pristine forest 10, Pristine grassland 11, Disturbed forest 6, Disturbed grassland 12.

Fig. S10

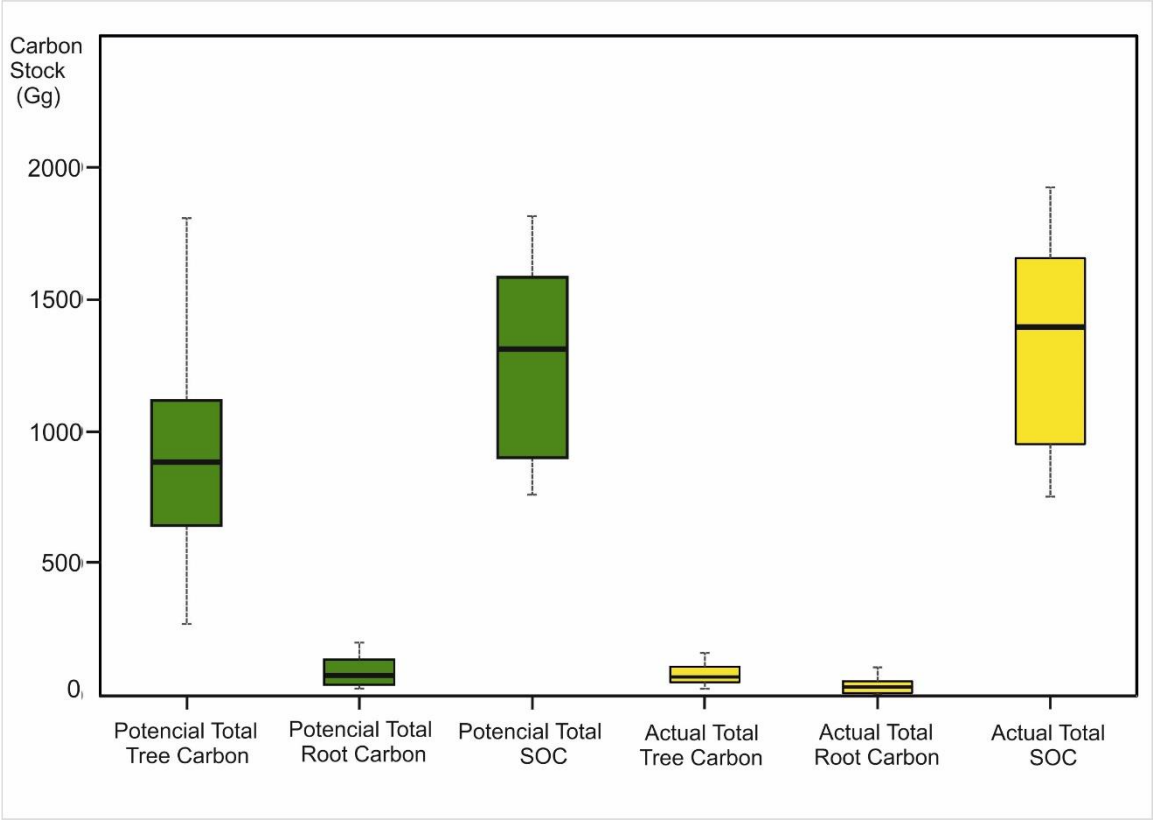

Fig. S10. Estimated values of the potential (green) and current (yellow) carbon stocks for aboveground tree carbon, root carbon and soil organic carbon (SOC) at the landscape scale for the high elevation area mapped of the Cordillera Urubamba (132,660 km^2). Values estimated using carbon stock values from pristine and disturbed forest and grassland (Table S16) extrapolated over the areas calculated using landscape mapping (Table S2-3, 18). Actual values of the carbon stocks can be found in Table S18.

Table S1.

Table S1. Mean climate values of the Cordillera Urubamba and Vilcabamba averaging all datalogger sources. Urubamba values based on 12 dataloggers placed at sites 1-4 with recordings made between Oct 2010-July 2012. Vilcabamba values based on 7 dataloggers placed at sites 5, 6 and 8 with recordings made between May 2012-April 2013. Site 5, although belonging to the Cordillera Urubamba, had a climate more similar to that of the Cordillera Vilcabamba with a correspondingly similar vegetation, and so is treated here as such.

	Absolute minimum temperature (øC)	Absolute maximum temperature (øC)	Mean daily minimum temperature (øC)	Mean daily maximum temperature (øC)	Mean daily temperature (øC)	Mean daily temperature variation	Absolute max daily temperature variation	Days yr where max temperature doesn't reach 5øC	Days yr where temperature dropped equal or below 0øC	Absolute minimum relative humidity (%)	Mean daily relative humidity (%)	Days yr where relative humidity passed 90%	Days yr with fog occurrence (relative humidity passed 99%)
Urubamba	-3.9	27.3	0.6	11.7	4.6	11.1	27.9	34.0	167.8	20.3	84.7	261.3	180.9
Vilcabamba	-6.4	17.6	1.2	8.7	4.1	7.5	19.2	25.1	88.1	24.1	90.7	299.3	207.3

Table S2.

Table S2. Overall values calculated from landscape mapping of vegetation from accessible (disturbed) and inaccessible (pristine) areas of the Cordillera Urubamba.

Human impact	class	Area (m2)	Percentage
Pristine	Grassland	419895	28.23
	Forest	995240	66.90
	Azonal	72496	4.87
	Total	1487631	
Disturbed	Grassland	69804605	53.22
	Forest	5669958	4.32
	Azonal	55697814	42.46
	Total	1.31E+08	

Table S3.

Table S3. Proportions of zonal vegetation that are occupied by forest or grassland from pristine and disturbed areas of the Cordillera Urubamba. Calculated using the values from Table S2.

Habitat type	Percentage cover
Pristine forest	70.33
Pristine grassland	29.67
Disturbed forest	7.51
Disturbed grassland	92.49

Table S4.

Table S4. GLMM analysis results of the effect of human impact, vegetation type and the interaction between human impact and vegetation type on different vegetation type structure properties. Conducted using R package 'glmmADMB' version 0.8.0.

Vegetation type structure property	Effect	Estimate	Std. Error	z value	Pr(>|z|)
Proportion of standing deadwood trees per 10x10m plot	(Intercept)	3.547	0.158	-22.5	<2e-16***
	Human impact	-1.477	0.197	-7.48	7.4e-14***
Average height of forb communities per 2x2m2 plot	(Intercept)	3.3186	0.0806	41.15	<2e-16***
	Human impact	-1.3264	0.075	-17.68	<2e-16***
	Vegetation type	0.2849	0.0818	3.48	0.0005***
	Interaction	-0.6249	0.1189	-5.25	1.50e-07***
Maximum height of forb communities per 2x2m2 plot	(Intercept)	4.3573	0.0577	75.54	<2e-16***
	Human impact	-0.7631	0.0541	-14.1	<2e-16***
	Vegetation type	0.0702	0.0596	1.18	0.239
	Interaction	-0.1432	0.0851	-1.68	0.093.
Cover of bare soil per 2x2m2 plot	(Intercept)	-3.3246	0.1213	-27.4	<2e-16***
	Human impact	1.3039	0.0987	13.21	<2e-16***
	Vegetation type	0.1842	0.1048	1.76	0.079.
	Interaction	-0.2694	0.15	-1.8	0.073.
Cover of litter per 2x2m2 plot	(Intercept)	0.0914	0.2165	0.42	0.67
	Human impact	-2.2581	0.125	-18.06	<2e-16***
	Vegetation type	0.1975	0.138	1.43	0.15
	Interaction	-0.8766	0.1966	-4.46	8.20e-06***

Table S5.

Table S5. LMM analysis results of the effect of human impact on forest structure properties. If values were transformed prior to analysis, the type of transformation is shown in brackets alongside the name of the property. Conducted using R package 'lmerTest' version 1.0.

Vegetation type structure property	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
Total aboveground biomass of trees per 10x10m plot (log10)	(Intercept)	7.6985	0.1944	1.24	39.609	0.00716 **
	Human impact	0.434	0.1483	46	2.926	0.00531 **
Average aboveground biomass of trees per 10x10m plot	(Intercept)	100.187	3.76	0.71	26.643	0.0611 .
	Human impact	5.249	2.209	40.67	2.376	0.0223 *
Max. aboveground biomass of trees per 10x10m plot	(Intercept)	111.893	3.844	0.86	29.108	0.0347 *
	Human impact	9.396	1.776	43.57	5.292	3.75e-06 ***
Stand basal area (log10)	(Intercept)	5.8983	0.3345	1.09	17.633	0.0288 *
	Human impact	1.0061	0.1621	45.62	6.207	1.46e-07 ***
Mean dbh of trees per 10x10m plot (log10)	(Intercept)	2.5791	0.2694	1.09	9.573	0.0551 .
	Human impact	0.2543	0.1192	42.22	2.134	0.0387 *
Mean height of trees per 10x10m plot (log10)	(Intercept)	1.5383	0.13768	4.19	11.173	0.000284 ***
	Human impact	0.31495	0.09821	42.29	3.207	0.002556 **
Max. height of trees per 10x10m plot (log10)	(Intercept)	2.7461	0.2114	3.62	12.987	0.000362 ***
	Human impact	0.7302	0.1241	41.16	5.883	6.26e-07 ***

Table S6.

Table S6. GLMM analysis results on the effect of human impact, vegetation type and the interaction between human impact and vegetation type on different biodiversity properties. Conducted using R package 'glmmADMB' version 0.8.0.

Ecosystem property	Effect	Estimate	Std. Error	z value	Pr(>|z|)
Vascular plant species richness per 2x2m^2 plot	(Intercept)	2.1944	0.0571	38.45	<2e-16***
	Human impact	0.8904	0.0451	1.97E+01	<2e-16***
	Vegetation type	0.0407	0.056	0.73	0.47
	Interaction	0.0641	0.0721	0.89	0.37
Cover of undescribed spp. per 2x2m^2 plot	(Intercept)	-0.445	0.334	-1.34	0.182
	Human impact	-2.868	0.21	-1.37E+01	<2e-16***
	Vegetation type	-0.469	0.232	-2.02	0.043*
	Interaction	0.456	0.33	1.38	0.167
Proportion of undescribed species per 2x2m^2 plot	(Intercept)	20.69	1.75	11.8	<2e-16***
	Human impact	-17.69	1.78	-9.94	<2e-16***
	Vegetation type	-2.47	1.71	-1.45	0.15
	Interaction	2.5	2.78	0.9	0.37
Cover of introduced species per 2x2m^2 plot	(Intercept)	-3.6649	0.0658	-55.69	<2e-16***
	Human impact	0.4478	0.0429	10.44	<2e-16***
	Vegetation type	0.0197	0.0465	0.42	0.6722
	Interaction	-0.2055	0.0675	-3.04	0.0023**
Proportion of introduced species per 2x2m^2 plot	(Intercept)	-3.6709	0.1063	-34.53	<2.00e-16***
	Human impact	0.8355	0.0601	13.91	<2.00e-16***
	Vegetation type	0.0296	0.0663	0.45	0.65511
	Interaction	-0.3538	0.0945	-3.74	0.00018***
Average latitudinal range size of vascular plant species per 2x2m^2 plot	(Intercept)	6.8052	0.0583	116.8	<2.00e-16***
	Human impact	0.7798	0.0481	16.22	<2.00e-16***
	Vegetation type	0.4188	0.053	7.9	2.80e-05***
	Interaction	-0.308	0.0758	-4.06	4.90e-0.5***
Epiphytic lichen species richness per 600cm^2 plot	(Intercept)	1.9965	0.1899	10.51	<2e-16***
	Human impact	-0.6461	0.0698	-9.26	<2e-16***

Table S7.

Table S7. Results of two-way ANOVA with interaction analyses on the effect of human impact, vegetation type and the interaction between human impact and vegetation type on Sorensen dissimilarity between sites. Conducted using R software.

Ecosystem property	Degrees of freedom	Effect	Sum of squares	Mean square	F-ratio	Pr(>F)
Sorensen dissimilarity between sites	1	Human impact	0.248	0.24801	14.527	0.00023 ***
	1	Vegetation type	0.0981	0.09813	5.748	0.01823 *
	1	Interaction	0.0377	0.03765	2.205	0.14043
	108	Residuals	1.8438	0.01707		

Table S8.

Table S8. List of undescribed species with the habitat type where predominantly found and associated indval value. Pristine forest, where the majority of undescribed species were found, is highlighted in grey. Collections made by SPS are also noted which are placed in CUZ, Z and LPB. Species with significant ($p < 0.05$) indval values are highlighted in bold. Signif. codes: '***'=$p<0.001$, '**'=$p<0.01$,'*'=$p<0.05$.

Family	New species to science	Habitat type where predominantly found	indval value	Collections from study area (S.P. Sylvester …)
Asteraceae	*Senecio* sp.nov.	Pristine forest	**0.13****	1458, 1604, 1865, 2111
Caprifoliaceae	*Valeriana* sp.nov.	Pristine forest	**0.10*****	240, 1418, 1465, 1519, 1866, 1872, 1879, 2110
Caryophyllaceae	*Stellaria* sp.nov.	Pristine forest	0.01	682, 1688
Orobanchaceae	*Bartsia lydiae* S.P. Sylvester	Pristine forest	0.02	127, 464, 680, 815, 878, 939, 1017, 1026, 1407, 1649, 1730, 1754
Poaceae	*Calamagrostis* sp.nov. 1	Pristine forest	**0.18*****	664, 692, 803, 1015, 1048, 1289, 1290
Poaceae	*Festuca linigluma* J.C. Ospina, S.P. Sylvester & M.D.P.V. Sylvester	Pristine forest	**0.17****	745, 778, 802, 871, 890, 1014, 1047, 1100, 1264, 1291, 1325, 1633, 1644, 2244
Poaceae	*Festuca proceroides* J.C. Ospina & S.P. Sylvester	Pristine forest	**0.15*****	233, 257, 295, 330, 353, 1420, 1421, 1455, 1506, 1507, 1583, 1848, 1898, 1899, 1902, 1903, 1908, 2120, 2139, 2200
Poaceae	*Poa urubambensis* S.P. Sylvester & Soreng	Pristine forest	**0.07****	812, 869, 1317, 1636, 1637, 1695, 403, 1727
Poaceae	*Calamagrostis* sp.nov. 2	Pristine grassland	0.01	1053, 1067, 1906
Poaceae	*Festuca calcana* J.C. Ospina & S.P. Sylvester	Pristine grassland	0.01	387, 1204, 1680
Polypodiaceae	*Moranopteris inaccessa* Sundue & S.P. Sylvester	Pristine grassland	0.01	300, 1628a
Asteraceae	*Werneria* sp.nov.	Disturbed forest	**0.04***	197, 603, 617, 1055, 1078
Campanulaceae	*Lysipomia mitsii* S.P. Sylvester & D. Quandt	Disturbed grassland	**0.27*****	823, 1417
Gentianaceae	*Gentianella viridiflora* S. Pfanzelt & S.P. Sylvester	Disturbed grassland	**0.16*****	1951
Iridaceae	*Cardenanthus* sp.nov.	Disturbed grassland	**0.33*****	855, 1383, 1416

Table S9.

Table S9. Comparison between the four habitat types of the number of significant ($p < 0.05$) vascular plant indicator species following indval analysis, and the proportion of this number which are undescribed or introduced.

Habitat type	Total No. of indicator species	Proportion of undescribed species as indicators (%)	Proportion of introduced species as indicators (%)
Pristine Forest	24	25	0
Pristine Grassland	20	0	0
Disturbed Forest	57	3.5	10.5
Disturbed Grassland	82	2.4	0

Table S10.

Table S10. Indval values for different species of vascular plant comparing pristine and disturbed forest and grassland habitat. Species with significant (p <0.05) indval values are in bold. Undescribed species are highlighted in yellow and introduced species are highlighted in blue. Signif. codes: '***'=p<0.001, '**'=p<0.01,'*'=p<0.05, '.'=p<0.1.

Indicator species	Pristine forest	Indicator species	Pristine grassland
Polylepis subsericans **J.F.Macbr.**	**0.31*** **	***Calamagrostis tarmensis*** **Pilg.**	**0.30*** **
Ourisia chamaedrifolia **Benth.**	**0.21*** **	***Perezia pungens*** **(Bonpl.) Less.**	**0.14*** **
Luzula gigantea **Desv.**	**0.21*** **	***Valeriana micropterina*** **Wedd.**	**0.13*** **
Gynoxys nitida **Muschl.**	**0.19*** **	***Bartsia thiantha*** **Diels**	**0.12*** **
Calamagrostis **sp.nov. 1**	**0.18*** **	***Baccharis johnwurdackiana*** **H. Rob.**	**0.12*** **
Pentacalia dictyophlebia **(Greenm.) Cuatrec.**	**0.18*** **	***Pernettya prostrata*** **(Cav.) DC.**	**0.11*** **
Ribes brachybotrys **(Wedd.) Jancz.**	**0.16*** **	***Baccharis tola*** **Phil.**	**0.11*** **
Festuca proceroides **J.C. Ospina & S.P. Sylvester sp.nov.**	**0.15*** **	***Achyrocline alata*** **(Kunth) DC.**	**0.09*** **
Calamagrostis intermedia **(J. Presl) Steud.**	**0.13*** **	***Calamagrostis recta*** **(Kunth) Trin. ex Steud.**	**0.09*** **
Cerastium subspicatum **Wedd.**	**0.12*** **	***Austrolycopodium magellanicum*** **(P. Beauv.) Holub**	**0.06****
Valeriana **sp.nov.**	**0.10*** **	***Carex pichinchensis*** **Kunth**	**0.10***
Bomarea dulcis **(Hook.) Beauverd**	**0.23***	***Calamagrostis rigida*** **(Kunth) Trin. ex Steud.**	**0.09***
Festuca linigluma **J.C. Ospina, S.P. Sylvester & M.D.P.V. Sylvester sp.nov.**	**0.17***	***Valeriana mandoniana (Wedd.) Höck***	**0.07***
Senecio praeruptorum **Sch. Bip. ex Klatt**	**0.13***	***Niphogeton dissecta*** **(Benth.) J.F. Macbr.**	**0.06***
Senecio **sp.nov.**	**0.13***	***Ranunculus krapfia*** **DC. Ex Deless**	**0.05***
Gynoxys cuzcoensis **Cuatrec.**	**0.11***	***Misbrookea strigosissima*** **(A. Gray) V.A. Funk**	**0.04***
Chersodoma antennaria **(Wedd.) Cabrera**	**0.10***	***Hieracium streptochaetum*** **Zahn**	**0.03***
Senecio rhizomatus **Rusby**	**0.08***	***Senecio melanocalyx*** **Cuatrec.**	**0.02***
Melpomene peruviana **(Desv.) A.R. Sm. & R.C. Moran**	**0.07***	***Lysipomia glandulifera*** **(Schltdl. ex Wedd.) Schltdl. ex E. Wimm.**	**0.02***
Oxalis phaeotricha **Diels**	**0.07***	***Calceolaria virgata*** **Ruiz & Pav.**	**0.02***
Poa urubambensis **S.P.Sylvester & Soreng sp.nov.**	**0.07***	*Berberidaceae* sp.1	0.02.
Senecio hohenackeri **Sch. Bip.**	**0.07***	*Polystichum cochleatum* (Klotzsch) Hieron.	0.02.
Gentianella scarlatiflora **(Gilg) J.S.Pringle**	**0.04***	*Werneria villosa* A. Gray	0.05
Tristerix longebracteatus **(Desr.) Barlow & Wiens**	**0.04***	*Anatherostipa hans meyeri* (Pilg.) Peñail.	0.04
Poa cf.huancavelicae Tovar	0.06.	*Werneria orbignyana* Wedd.	0.04
Agrostis perennans (Walter) Tuck.	0.05.	*Senecio chrysolepis* Phil.	0.04
Bartsia flava Molau	0.04.	*Ageratina glechonophylla* (Less.) R.M. King. H. Rob.	0.03
Salpichroa glandulosa (Hook.) Miers	0.04	*Belonanthus hispidus* (Wedd.) Graebn.	0.03
Fuchsia apetala Ruiz & Pav.	0.03	*Halenia phyteumoides* Gilg (syn.= Halenia weberbaueri C.K. Allen)	0.02
Melpomene personata Lehnert	0.02	*Achyrocline ramosissima* Britton	0.02
Bartsia lydiae S.P. Sylvester sp.nov.	0.02	*Senecio genisianus* Cuatrec.	0.02
Senecio hastatifolius Cabrera	0.02	*Poa cf.trollii* (Pilg.) Refulio (syn. = Dissanthelium trollii Pilg.)	0.01

Indicator species	Pristine forest	Indicator species	Pristine grassland
Baccharis caespitosa (Ruiz &Pav.) Pers.	0.02	*Werneria plantaginifolia* Wedd. ex Klatt	0.01
Festuca. sp.1	0.01	*Gentianella thyrsoidea* (Hook.) Fabris	0.01
Bartsia elongata Wedd.	0.01	*Senecio flaccidifolius* Wedd.	0.01
Belloa schultzii (Wedd.) Cabrera	0.01	*Saxifraga magellanica* Poir.	0.01
Senecio adenophyllus Meyen. Walp.	0.01	*Caiophora contorta* (Desr.) C. Presl	0.01
Jamesonia imbricata (Sw.) Hook. & Grev.	0.01	*Senecio nutans* Sch.Bip.	0.01
Stellaria sp.nov.	0.01	*Werneria staticifolia* Sch.Bip.	0.01
Erigeron rosulatus Wedd.	0.01	*Calamagrostis* sp.nov. 2	0.01
Berberis saxicola Lechler	0.01	*Miconia chionophila* Naudin	0.01
Calamagrostis cf.polygama (Griseb.) Parodi	0.01	*Campyloneurum asplundii* (C. Chr.) Ching	0.01
Lasiocephalus lingulatus Schltdl.	0.01	*Moranopteris inaccessa* Sundue & S.P. Sylvester sp.nov.	0.01
Loricaria thuyoides (Lam.) Sch.Bip.	0.01	*Valeriana radicata* Graebn.	0.01
Sisyrinchium palmifolium L.	0.01	*Chaptalia rotundifolia* D. Don	0.01
Silene andicola Gillies ex Hook. & Arn.	0	*Olsynium junceum* (E. Mey. ex C. Presl) Goldblatt	0.01
		Festuca calcana J.C. Ospina & S.P. Sylvester sp.nov.	0.01
Indicator species	**Disturbed forest**	**Indicator species**	**Disturbed grassland**
***Poa horridula* Pilg.**	**0.42*** **	***Lachemilla pinnata* (Ruiz & Pav.) Rothm.**	**0.50*** **
***Polylepis racemosa* Ruiz & Pav.**	**0.31*** **	***Geranium sessiliflorum* Cav.**	**0.47*** **
***Oreomyrrhis andicola* (Kunth) Endl. ex Hook. f.**	**0.29*** **	***Hypochaeris meyeniana* (Walp.) Benth. & Hook. f. ex Griseb.**	**0.46*** **
***Azorella multifida* (Ruiz & Pav.) Pers.**	**0.26*** **	***Calamagrostis vicunarum* (Wedd.) Pilg.**	**0.44*** **
***Polylepis pepei* B.B. Simpson**	**0.24*** **	***Luzula racemosa* Desv.**	**0.44*** **
***Gunnera magellanica* Lam.**	**0.23*** **	***Gamochaeta americana* (Mill.) Wedd.**	**0.39*** **
***Urtica magellanica* Juss. ex Poir.**	**0.23*** **	***Sisyrinchium brevipes* Baker**	**0.37*** **
***Poa annua* L.**	**0.22*** **	***Oxalis oreocharis* Diels**	**0.37*** **
***Gentianella rima* (D.Don ex G.Don) Fabris**	**0.21*** **	***Agrostis breviculmis* Hitchc.**	**0.36*** **
***Uncinia macrolepis* Decne.**	**0.21*** **	***Calamagrostis heterophylla* (Wedd.) Pilg.**	**0.35*** **
***Cotula mexicana* (DC.) Cabrera**	**0.20*** **	***Oenothera multicaulis* Ruiz & Pav.**	**0.33*** **
***Ranunculus repens* L.**	**0.19*** **	***Cardenanthus* sp.nov.**	**0.33*** **
***Werneria nubigena* Kunth**	**0.19*** **	***Aciachne acicularis* Lægaard**	**0.30*** **
***Geranium core core* Steud.**	**0.18*** **	***Lysipomia mitsii* S.P. Sylvester & D. Quandt sp.nov.**	**0.27*** **
***Poa gymnantha* Pilg.**	**0.18*** **	***Galium corymbosum* Ruiz & Pav.**	**0.27*** **
***Stellaria media* (L.) Vill.**	**0.16*** **	***Belloa piptolepis* (Wedd.) Cabrera**	**0.27*** **
***Stellaria weddellii* Pedersen**	**0.16*** **	***Carex ecuadorica* K.k.**	**0.26*** **
***Lachemilla andina* (L.M. Perry) Rothm.**	**0.16*** **	***Azorella biloba* (Schltdl.) Wedd.**	**0.24*** **
***Arenaria soratensis* Rohrb.**	**0.16*** **	***Crassula closiana* (Gay) Reiche**	**0.23*** **
***Baccharis alpina* Kunth**	**0.15*** **	***Peperomia verruculosa* Dahlst. ex A.W. Hill**	**0.22*** **
***Veronica arvensis* L.**	**0.15*** **	***Novenia acaulis* (Benth. & Hook. f. ex B.D. Jacks.) S.E. Freire & F.H. Hellw.**	**0.22*** **

Indicator species	Disturbed forest	Indicator species	Disturbed grassland
Sisyrinchium jamesonii Baker	0.13***	*Muhlenbergia peruviana* (P. Beauv.) Steud.	0.21***
Halenia umbellata (Ruiz & Pav.) Gilg	0.13***	*Cerastium crassipes* Bartl.	0.17***
Stellaria cuspidata Willd. ex Schltdl.	0.12***	*Lupinus microphyllus* Desr.	0.17***
Bromus lanatus Kunth	0.11***	*Paspalum pygmaeum* Hack.	0.17***
Senecio peruensis Cuatrec.	0.11***	*Gentianella peruviana* (Griseb.) Fabris	0.16***
Lysipomia laciniata A. DC.	0.11***	*Gentianella* sp.1	0.16***
Gentianella viridiflora S. Pfanzelt & S.P. Sylvester sp.nov.	0.08***	*Festuca casapaltensis* J.Ball	0.15***
Festuca tenuiculmis Tovar	0.06***	*Muehlenbeckia volcanica* (Benth.) Endl.	0.15***
Solanum tuberosum L.	0.06***	*Myrosmodes paludosum* (Rchb. f.) P. Ortiz	0.14***
Poa subspicata (J. Presl) Kunth	0.13*	*Cyperus seslerioides* Kunth	0.14***
Calamagrostis glacialis (Wedd.) Hitchc.	0.09*	*Calamagrostis rigescens* (J. Presl) Scribn.	0.13***
Plantago australis Lam.	0.07*	*Arenaria digyna* Willd. ex Schltdl.	0.12***
Belloa longifolia (Cuatrec.) Sagast. & Dillon	0.07*	*Poa serpaiana* Refulio	0.11***
Agrostis tolucensis Kunth	0.07*	*Ophioglossum crotalophoroides* Walter	0.10***
Perezia ciliosa (Phil.) Reiche	0.06*	*Plantago lamprophylla* Pilg.	0.10***
Carex bonplandii Kunth	0.06*	*Lachemilla aphanoides* (Mutis ex L. f.) Rothm.	0.09***
Erigeron cf.chionophilus Wedd.	0.06*	*Oxalis nubigena* Walp.	0.08***
Astragalus uniflorus DC.	0.06*	*Lupinus herzogii* Ulbr.	0.08***
Werneria pectinata Lingelsh.	0.05*	*Aphanactis villosa* S. F. Blake	0.08***
Polystichum nudicaule Rosenst.	0.05*	*Poa macusaniensis* (E.H.L. Krause) Refulio	0.08***
Cystopteris fragilis (L.) Bernh.	0.05*	*Geranium sibbaldioides* Benth.	0.08***
Bromus modestus Renvoize	0.05*	*Lachemilla fulvescens (*L.M. Perry) Rothm.	0.07***
Senecio modestus Wedd.	0.05*	*Wahlenbergia peruviana* A.Gray	0.07***
Halenia caespitosa Gilg	0.05*	*Gentiana sedifolia* Kunth	0.07***
Cerastium glomeratum Thuill.	0.05*	*Gnaphalium melanosphaeroides* Sch. Bip. ex Wedd.	0.07***
Festuca soukupii Stanc.k	0.04*	*Trifolium amabile* Kunth	0.07***
Plagiobothrys humilis (Ruiz & Pav.) I.M. Johnst.	0.04*	*Solanum acaule* Bitter	0.07***
Cardamine bonariensis Pers.	0.04*	*Acaena cylindristachya* Ruiz & Pav.	0.05***
Valeriana pycnantha A. Gray	0.04*	*Oreobolopsis tepalifera* T. Koyama & Guagl.	0.18**
Werneria caespitosa Wedd.	0.04*	*Perezia pinnatifida* (Bonpl.) Wedd.	0.10*
Werneria sp.nov.	0.04*	*Werneria pygmaea* Gillies ex Hook. & Arn.	0.08*
Lachemilla orbiculata (Ruiz & Pav.) Rydb.	0.04*	*Gentianella cf.persquarrosa* (Reimers) J.S. Pringle	0.08*
Capsella bursa pastoris (L.) Medik.	0.03*	*Poa perligulata* Pilg.	0.07*
Hydrocotyle filipes Mathias	0.03*	*Festuca cf.rigescens* (J. Presl) Kunth	0.07*
Asplenium castaneum Schltdl. & Cham.	0.03*	*Bartsia peruviana* Walp.	0.07*
Bromus catharticus Vahl	0.03*	*Calandrinia acaulis* Kunth	0.07*
Oritrophium hieracioides (Wedd.) Cuatrec.	0.06.	*Tarasa urbaniana* (Ulbr.) Krapov.	0.06*
Lachemilla tanacetifolia Rothm.	0.04.	*Hordeum muticum* J. Presl	0.06*

Indicator species	Disturbed forest	Indicator species	Disturbed grassland
Montia fontana L.	0.03.	***Hypochaeris taraxacoides* Ball**	**0.06***
Plantago rigida Kunth	0.03.	***Aphanes parvula* Gutte**	**0.06***
Poa swallenii Refulio	0.03.	***Muhlenbergia ligularis* (Hack.) Hitchc.**	**0.06***
Draba cuzcoensis O.E.Schulz	0.03.	***Lupinus pulvinaris* Ulbr.**	**0.06***
Veronica opaca Fr.	0.02.	***Belloa kunthiana* (DC.) Anderb. & S.E. Freire**	**0.06***
Nototriche longirostris (Wedd.) A.W. Hill	0.02.	***Berberis lutea* Ruiz & Pav.**	**0.05***
Castilleja virgatoides Edwin	0.04	***Castilleja pumila* (Benth.) Wedd.**	**0.05***
Baccharis papillosa Rusby	0.03	***Senecio candollei* Wedd.**	**0.05***
Festuca dolichophylla J.Presl	0.03	***Nassella mexicana* (Hitchc.) R.W. Pohl**	**0.05***
Nassella inconspicua (J. Presl) Barkworth	0.02	***Perezia multiflora* (Bonpl.) Less.**	**0.04***
Noticastrum marginatum (H.B.K.) Cuatr.	0.02	***Facelis plumosa* (Wedd.) Sch.Bip.**	**0.04***
Werneria aretioides Wedd.	0.02	***Paronychia muschleri* Chaudhri**	**0.04***
Vulpia myuros (L.) C.C. Gmel.	0.02	***Bartsia pauciflora* Molau**	**0.03***
Calceolaria engleriana Kraenzl.	0.02	***Carex boliviensis* Van Heurck & M.ll. Arg.**	**0.03***
Polypodium chrysolepis Hook.	0.02	***Calamagrostis amoena var. festucoides* (Wedd.) Soreng**	**0.03***
Brayopsis alpaminae Gilg & Muschl. subsp. alpaminae	0.02	***Bidens andicola* Kunth**	**0.03***
Thelypteris	0.02	***Calceolaria scapiflora* (Ruiz & Pav.) Benth.**	**0.03***
Trisetum spicatum (L.) K. Richt.	0.02	***Hypericum brevistylum* Choisy**	**0.03***
Epilobium denticulatum Ruiz & Pav.	0.02	***Luciliocline subspicata* (Wedd.) Anderb. & S.E.Freire**	**0.03***
Mimulus glabratus Kunth	0.02	***Urtica flabellata* Kunth**	**0.03***
Valeriana mandonii Britton	0.02	***Poa calycina* (J. Presl) Kunth**	**0.03***
Poa infirma Kunth	0.02	***Trichophorum rigidum* (Boeckeler) Goetgh. Muasya & D.A. Simpson**	**0.03***
Cerastium mollissimum Poir.	0.01	***Crassula connata* (Ruiz & Pav.) A.Berger**	**0.03***
Draba werffii Al Shehbaz	0.01	*Gnaphalium badium* Wedd.	0.04.
Bowlesia flabilis J.F. Macbr.	0.01	*Lepidium abrotanifolium* Turcz.	0.03.
Senecio canescens (Humb. & Bonpl.) Cuatrec.	0.01	*Lupinus soratensis* Rusby	0.02.
Plantago tubulosa Decne.	0.01	*Hedeoma mandoniana* Wedd.	0.02.
Polystichum orbiculatum (Desv.) J. Rémy & Fée	0.01	*Gamochaeta purpurea* (L.) Cabrera	0.02.
Oritrophium sp.	0.01	*Festuca peruviana* Infantes	0.02.
Aciachne pulvinata Benth.	0.01	*Festuca asplundii* E.B. Alexeev	0.02.
Urtica urens L.	0.01	*Distichia muscoides* Nees. Meyen.	0.02.
Hypochaeris sessiliflora Kunth	0.01	*Castilleja nubigena* Kunth	0.02.
Calamagrostis ovata (J. Presl) Steud.	0.01	*Carex jamesonii* Boott	0.02.
Ribes bolivianum Jancz.	0.01	*Alstroemeria pygmaea* Herb.	0.02.
Clinopodium brevicalyx (Epling) Harley & A.Granda	0.01	*Agrostis trichodes* (Kunth) Roem. & Schult.	0.02.
Oxalis conorrhiza Jacq.	0.01	*Acaena elongata* L.	0.02.
Colobanthus quitensis (Kunth) Bartl.	0.01	*Paranephelius ovatus* A.Gray ex Wedd.	0.02
Senecio sp.1	0.01	*Lupinus chlorolepis* C.P. Sm.	0.02

Indicator species	Disturbed forest	Indicator species	Disturbed grassland
Phyllactis pulvinata Rauh. Willer	0.01	*Oritrophium limnophilum* (Sch.Bip.) Cuatrec.	0.02
Asplenium haenkeanum (C. Presl) Hieron.	0.01	*Bartsia pyricarpa* Molau	0.02
Asplenium peruvianum Desv.	0.01	*Arcytophyllum filiforme* (Ruiz & Pav.) Standl.	0.02
Festuca humilior Nees. Meyen	0.01	*Rumex acetosella* L.	0.01
Elaphoglossum mathewsii (Fée) T. Moore	0.01	*Veronica serpyllifolia* L.	0.01
Melpomene moniliformis (Lagasca ex. Sw.) A.R.Sm. & R.C.Moran	0.01	*Bartsia stricta* (Kunth) Benth.	0.01
Elaphoglossum hartwegii (Fée) T. Moore	0.01	*Microsteris gracilis* (Douglas ex Hook.) Greene	0.01
Cardamine vulgaris Phil.	0.01	*Eleocharis albibracteata* Nees & Meyen ex Kunth	0.01
Descurainia myriophylla (Willd. ex DC.) R.E. Fr. (Synonym= D.mabridei O.E. Schulz)	0.01	*Woodsia montevidensis* (Spreng.) Hieron.	0.01
*Calamagrostis orbignyana (*Wedd.) Wedd. ex Pilg.	0	*Gamochaeta longipedicellata* Cabrera	0.01
Uncinia phleoides (Cav.) Pers.	0	*Viola pygmaea* Juss. ex Poir	0.01
		Phlegmariurus crassus (Humb. & Bonpl. ex Willd.) B. Øllg.	0.01
		Lachemilla vulcanica (Schltdl. & Cham.) Rydb.	0.01
		Taraxacum officinale F.H. Wigg.	0.01
		Asteraceae sp.3	0.01
		Plagiobothrys congestus (Wedd.) I.M. Johnst.	0.01
		Potentilla dombeyi Nestl.	0.01
		Asplenium stoloniferum Bory	0.01
		Calamagrostis spicigera (J. Presl) Steud.	0.01
		Festuca inarticulata Oilg.	0.01
		Calamagrostis sp.3	0.01
		Cicendia quadrangularis (Dombey ex Lam.) Griseb.	0.01
		Soliva sessilis Ruiz & Pav.	0.01
		Calamagrostis fiebrigii Pilg.	0.01
		Peperomia sp.2	0.01
		Peperomia sp.1	0.01
		Descurainia athrocarpa (A. Gray) O.E. Schulz	0.01
		Lysipomia sphagnophila Griseb. ex Wedd.	0.01
		Senecio evacoides Sch.Bip. ex Wedd.	0.01
		Calamagrostis sclerantha Hack.	0.01
		Cotula australis (Sieber ex Spreng.) Hook. f.	0.01
		Agrostis meyenii Trin.	0.01
		Lupinus ballianus C.P. Sm.	0.01
		Ribes cuneifolium Ruiz & Pav.	0.01
		Brayopsis calycina (Desv.) Gilg & Muschl.	0
		Ephedra rupestris Benth.	0

Table S11.

Table S11. Indval values for different epiphytic lichen species comparing standing deadwood and live tree habitat. Species with significant ($p < 0.05$) indval values are highlighted in bold. Signif. codes: '***'=p<0.001, '**'=p<0.01,'*'=p<0.05, '.'=p<0.1.

Indicator species	Deadwood	Indicator species	Live
Parmelinopsis subfatiscens **(Kurok.) Elix & Hale**	**0.29*** **	*Cetrariastrum* sp.	0.03.
Normandina pulchella **(Borrer) Nyl.**	**0.26*** **	*Hypotrachyna bogotensis* (Vain.) Hale	0.02.
Ramalina reducta **Krog & Swinscow**	**0.23*** **	*Usnea* sp.1	0.06
Heterodermia parva **Morbeg**	**0.22*** **	*Cladonia borbonica* Nyl.	0.04
Usnea fulvoreagens **(Räsänen) Räsänen**	**0.2*** **	*Chaenotheca brunneola* (Ach.) Müll. Arg.	0.04
Caloplaca **sp.1**	**0.2*** **	*Chaenotheca furfuracea* (L.) Tibell	0.04
Leptogium resupinans **Nyl.**	**0.2*** **	*Buellia rhizocarpica* Etayo, Giralt & Elix.	0.03
Rinodina **sp.**	**0.18*** **	*Parmeliella incrassata* P.M. Jørg.	0.03
Bacidia **sp.**	**0.14*** **	*Chaenotheca cf chrysocephala* (Turner ex Ach.) Th. Fr.	0.02
Heterodermia magellanica **(Zahlbr.) Winsc. & Krog**	**0.09*** **	*Cladonia pocillum* (Ach.) O.J. Rich.	0.02
Chaenotheca chrysocephala **(Turner ex Ach.) Th. Fr.**	**0.21** **	*Sticta laevis* (Nyl.) Vain.	0.02
Buellia **sp.1**	**0.17** **	*Sticta albocyphellata* Moncada & Lücking sp.nov.	0.02
Oropogon bicolor **Essl.**	**0.14** **	*Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng.	0.02
Cetrariastrum dubitans **Sipman**	**0.12** **	*Sticta paralimbata* Moncada & Lücking sp.nov.	0.02
Pannaria rubiginosa **(Thunb. ex Ach.) Delise**	**0.09** **	*Botryolepraria neotropica* Kukwa & Pérez-Ortega	0.02
Amandinea **sp.1**	**0.08** **	*Cladonia subradiata* (Vain.) Sandst.	0.01
Sp.1	**0.07** **	*Sticta dioica* Moncada & Lücking sp. nov.	0.01
Cetrariastrum equadoriense **(R.Sant.) Sipman**	**0.13***	*Chaenotheca cf chlorella* (Ach.)Müll.Arg.	0.01
Lecidea **sp.1**	**0.1***	*Coenogonium aff luteolum* (Kalb) Kalb & Lücking	0.01
Leptogium andinum **P.M. Jørg.**	**0.09***	*Dictyonema glabratum* (Spreng.) D. Hawksw.	0.01
Oropogon loxensis **(Fée) Zukal**	**0.09***	*Gyalideopsis* sp.	0.01
Melanohalea subolivacea **(Nyl. ex Hasse) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch**	**0.08***	*Hypogymnia* sp.	0.01
Buellia **sp.2**	**0.08***	*Hypotrachyna longiloba* (H. Magn.) C.W.Sm.	0.01
Oropogon **sp.1**	**0.07***	*Pertusaria subambigens* Dibben	0.01
Collema glaucophthalmum **Nyl.**	**0.06***	*Phyllopsora* sp.	0.01
Scoliciosporum **sp.**	**0.05***	Sp.7	0.01
Buellia **sp.4**	**0.04***	*Hypotrachyna* sp.	0.01
Ochrolechia africana **Vain.**	**0.03***	*Peltigera fibrilloides* (Gyeln.) Vitik.	0.01
Arthonia sp.1	0.09.	*Hypotrachyna meyeri* (Zahlbr.) Streimann	0.01
Leptogium punctulatum Nyl.	0.06.	*Chrysothrix* sp.	0.01
Opegrapha sp.	0.05.	*Parmelina cleefii* Sipman	0.01
Biatora sp.	0.04.	*Sticta tomentosa* (Sw.) Ach.	0.01
Agonimia tristicula (Nyl.) Zahlbr.	0.03.	*Sticta atroandensis* Moncada & Lücking sp.nov.	0.01

Indicator species	Deadwood	Indicator species	Live
Cetrariastrum andense (Kärnefelt) Sipman	0.09	*Dimerella pineti* (syn = Coenogonium pineti (Ach.) Lücking & Lumbsch) (Ach.) Vězda	0.01
Usnea wasmuthii Räsänen	0.08	*Sticta brevior* Moncada & Lücking sp.nov.	0.01
Leptogium cochleatum (Dicks.) P.M. Jørg. & P. James	0.08	*Sticta marilandia* Moncada & Lücking sp.nov.	0.00
Sticta sp.5	0.08	*Hypotrachyna sinuosa* (Sm.) Hale	0.00
Sticta sp.1	0.06	Sp.6	0.00
Lecanora sp.	0.06	*Sticta* sp.3	0.00
Usnea cornuta (syn=*Usnea dasaea* Stirt.)Körb.	0.05	*Cladonia merochlorophaea* Asahina	0.00
Psoroma hypnorum (Vahl) Gray	0.04	*Sticta sylvatica* (Huds.) Ach.	0.00
Leptogium mandonii P.M. Jørg.	0.04		
Sticta sp.2	0.03		
Sticta andensis (Nyl.) Trevis.	0.03		
Usnea fragilescens Hav. ex Lynge	0.03		
Milospium sp.	0.02		
Usnea esperantiana P. Clerc	0.02		
Leptogium laceroides B. de Lesd.	0.02		
Remototrachyna sp.	0.02		
Leptogium phyllocarpum (Pers.) Mont.	0.02		
Leptogium menziesii (Sm.) Mont.	0.02		
Pertusaria sp.	0.02		
Caloplaca sp.2	0.02		
Chaenotheca chlorella (Ach.)Müll.Arg.	0.02		
Dimerella lutea (syn = *Coenogonium luteum* (Dicks.) Kalb & Lücking)(Dicks.) Trevis.	0.02		
Collema fasciculare (L.) Weber ex F.H. Wigg.	0.02		
Bacidina sp.	0.02		
Stereocaulon glareosum (Savicz) H. Magn.	0.02		
Leprocaulon congestum (Nyl.) I.M. Lamb & A. Ward	0.01		
Sp.5	0.01		
Candelariella sp.1	0.01		
Sticta sublimbatoides Moncada & Lücking. sp nov.	0.01		
Psorogalaena sp.	0.01		
Chaenothecopsis nivea (F. Wilson) Tibell	0.01		
Buellia proximata H. Magn.	0.01		
Lecidea sp.2	0.01		
Megalospora admixta (Nyl.) Sipman	0.01		
Megaspora verrucosa (Ach.) Hafellner & V. Wirth	0.01		
Sticta fuliginosa (Dicks.) Ach.	0.01		
Sticta maculofuliginosa Moncada & Lücking sp.nov.	0.01		
Sticta paramuna Moncada & Lücking sp.nov.	0.01		
Sp.3	0.01		

Indicator species	Deadwood	Indicator species	Live
Arthonia sp.2	0.01		
Hypotrachyna ensifolia (Kurok.) Hale	0.01		
Hypotrachyna sublaevigata (Nyl.) Hale	0.01		
Sp.4	0.01		
Porina sp.	0.01		
Chaenothecopsis pusilla (Ach.) A.F.W. Schmidt	0.01		
Leptogium burgessii (L.) Mont.	0.01		
Cladonia cartilaginea Müll. Arg.	0.00		
Chaenothecopsis debilis (Sm.) Tibell	0.00		
Buellia disciformis (Fr.) Mudd	0.00		
Candelariella sp.2	0.00		
Chysothrix sp.	0.00		
Cladonia sp.	0.00		
Leptogium coralloideum (Meyen & Flot.) Vain.	0.00		
Leptogium cyanescens (Pers.) Körb.	0.00		
Pannaria andina P.M. Jørg. & Sipman	0.00		
Sp.8	0.00		
Sticta rhizinata Moncada & Lücking sp.nov.	0.00		
Usnea glabrata (Ach.) Vain.	0.00		
Usnea setulosa Motyka	0.00		
Usnea sp.2	0.00		

Table S12.

Table S12. LMM analysis results of the effect of human impact, vegetation type and the interaction between human impact and vegetation type on plant trait syndromes represented by principal components. Conducted using R package 'lmerTest' version 1.0.

Principal component	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
PC1 'low-growing herbs'	(Intercept)	-0.01721	0.04361	9.1	-0.394	0.702
	Human impact	0.55008	0.02978	465.5	18.472	<2e-16 ***
	Vegetation type	0.29292	0.03294	465	8.892	<2e-16 ***
	Interaction	0.01966	0.04693	464.6	0.419	0.675
PC2 'tussock grasses'	(Intercept)	0.66583	0.07378	10.9	9.025	2.14e-06 ***
	Human impact	-0.62479	0.05387	466.3	-11.597	< 2e-16 ***
	Vegetation type	0.27328	0.0596	465.9	4.585	5.84e-06 ***
	Interaction	-0.29732	0.08491	465.6	-3.502	0.000507 ***
PC3 'trees'	(Intercept)	1.26177	0.07891	9.7	15.989	2.61e-08 ***
	Human impact	-0.74503	0.05051	465.3	-14.749	< 2e-16 ***
	Vegetation type	-0.9244	0.05588	464.8	-16.544	< 2e-16 ***
	Interaction	0.47708	0.07959	464.4	5.994	4.11e-09 ***
PC4 'geophytes'	(Intercept)	0.31543	0.09497	8.5	3.321	0.00959 **
	Human impact	-0.01624	0.04293	463	-0.378	0.7054
	Vegetation type	-0.34628	0.04747	462.6	-7.295	1.31e-12 ***
	Interaction	0.13247	0.0676	462.1	1.96	0.05065 .
PC5 'large creeping forbs'	(Intercept)	0.32513	0.06338	10.1	5.13	0.000431 ***
	Human impact	-0.55231	0.03913	465.2	-14.113	< 2e-16 ***
	Vegetation type	-0.17307	0.04329	464.8	-3.998	7.42e-05 ***
	Interaction	-0.03488	0.06166	464.3	-0.566	0.571909
PC6 'not large biennial herbs'	(Intercept)	-0.33607	0.04806	13.2	-6.993	8.72e-06 ***
	Human impact	0.17684	0.0413	467.4	4.282	2.25e-05 ***
	Vegetation type	-0.20814	0.0457	467	-4.554	6.71e-06 ***
	Interaction	0.26425	0.06511	467.2	4.059	5.78e-05 ***
PC7 'short graminoids'	(Intercept)	-0.03736	0.072	8.6	-0.519	0.617
	Human impact	0.1981	0.02771	462.3	7.149	3.43e-12 ***
	Vegetation type	-0.01022	0.03064	462.1	-0.334	0.739
	Interaction	-0.01131	0.04363	461.7	-0.259	0.796
PC8 'not spiny or cushion forming'	(Intercept)	0.04601	0.04777	8.7	0.963	0.361416
	Human impact	-0.08383	0.02276	463.3	-3.684	0.000257 ***
	Vegetation type	0.05182	0.02517	462.9	2.059	0.040021 *
	Interaction	-0.0577	0.03584	462.4	-1.61	0.108058

Table S13.

Table S13. Morphological traits and their corresponding scaled principal component loadings, eigenvalues and proportion of the data explained. Numbers in bold indicate high loadings.

Trait	PC1 'low-growing herbs'	PC2 'tussock grasses'	PC3 'trees'	PC4 'geo-phytes'	PC5 'large creeping forbs'	PC6 'not large biennial herbs'	PC7 'short gramin-oids'	PC8 'not spiny or cushion forming'
Moderately hairy	**1.04**	-0.45	0.06	-0.24	0.57	-0.12	0.23	-0.01
Densely hairy	0.10	-0.08	-0.08	0.13	-0.16	-0.20	-0.24	0.32
Spiny or stinging	0.12	-0.03	-0.04	-0.11	-0.25	-0.21	**-1.00**	**-1.13**
Sclerophyllous	0.35	**1.04**	0.26	**-0.80**	0.21	-0.28	-0.07	-0.35
Tussocks	0.09	**1.30**	0.28	-0.67	0.45	-0.11	-0.14	0.06
Graminoid	0.41	**1.19**	0.17	-0.31	-0.60	-0.54	**0.70**	-0.21
Below-ground storage organs	**0.73**	0.37	0.03	**0.80**	-0.34	0.41	-0.67	0.54
Rhizomatous	0.50	0.68	-0.06	**1.45**	0.07	0.19	0.23	-0.23
Buds close to soil level	**1.41**	-0.12	0.00	0.57	-0.11	0.04	-0.26	-0.14
Stoloniferous	**1.26**	-0.46	0.11	-0.27	**0.77**	-0.09	0.27	-0.13
Creeping	**1.27**	-0.50	0.10	-0.30	**0.75**	-0.08	0.30	-0.14
Rosette	0.49	-0.02	-0.03	0.13	**-0.86**	0.04	**-0.83**	0.44
Cushion forming	0.10	0.00	-0.01	-0.14	-0.17	-0.07	**-0.82**	**-1.26**
Prostrate	**1.44**	-0.43	0.07	0.04	0.44	0.11	0.05	0.13
Veg. height over 300cm	-0.22	-0.28	**1.75**	0.24	-0.04	-0.14	-0.01	-0.01
Veg. height 50-300cm	0.12	1.49	0.27	-0.15	0.65	0.31	-0.35	0.26
Veg. height 15-50cm	-0.22	-0.06	-0.23	0.26	0.41	**-1.44**	-0.43	0.35
Veg. height 5-15cm	-0.01	0.36	-0.14	**0.82**	0.05	-0.31	0.75	-0.64
Veg. height 0-5cm	**1.53**	-0.01	0.08	-0.15	**-0.79**	-0.18	0.07	0.15
Reproduct. height over 300cm	-0.22	-0.28	**1.75**	0.24	-0.04	-0.14	-0.01	-0.01
Reproduct. height 50-300cm	0.16	**1.53**	0.25	0.07	0.63	0.29	-0.20	0.10
Reproduct. height 15-50cm	-0.18	0.10	-0.26	0.67	0.34	**-1.35**	-0.04	-0.02
Reproduct. height 5-15cm	0.41	0.46	0.03	-0.23	**-1.18**	-0.43	**0.71**	-0.04
Reproduct. height 0-5cm	**1.51**	-0.38	0.05	0.03	0.00	0.13	-0.36	0.13
Epiphyte	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nanophanerophyte	-0.13	0.35	0.05	-0.13	0.44	0.35	-0.26	0.28
Micro-mesophanerophyte	-0.21	-0.28	**1.75**	0.24	-0.04	-0.15	-0.01	-0.01
Geophyte	0.53	0.65	-0.07	**1.48**	0.05	0.22	0.17	-0.19
Chamaephyte	0.50	-0.20	0.03	-0.20	0.55	-0.19	0.03	-0.26
Hemicryptophyte	**1.11**	0.55	0.18	**-0.71**	-0.69	-0.48	-0.07	0.23
Biennial	-0.12	-0.04	-0.15	0.24	0.33	**-1.20**	-0.36	0.44
Therophyte	0.26	-0.26	-0.05	-0.08	0.13	0.11	0.42	-0.12
Eigenvalue	5.048	3.630	2.986	2.686	2.285	2.167	1.735	1.475
Proportion Explained	0.163	0.117	0.096	0.087	0.074	0.070	0.056	0.048
Cumulative Proportion	0.163	0.280	0.376	0.463	0.537	0.607	0.663	0.710

Table S14.

Table S14. Soil types of the soil profiles studied at sites 1 to 4. PF=Pristine Forest, PG=Pristine Grassland, DF=Disturbed Forest, DG=Disturbed Grassland.

Site	Mollic Leptosol	Phaeozem	Umbrisol
1 (n = 9)	2 (PG, PF)	4 (2 PF, 2 PG)	3 (GG)
2 (n = 12)	-	8 (2 PF, 1PG, 3 GF, 2 GG)	4 (1 PF, 2 PG, 1GG)
3 (n = 12)	-	5 (3 PF, 2 GF)	7 (3 PG, 1GF, 3 GG)
4 (n = 6)	-	1 PF	5 (2 PG, 3 GG)
Total	2	18 (8 PF, 3 PG, 5 GF, 2GG)	19 (1 PF, 7 PG, 1 GF, 10 GG)

Table S15.

Table S15. LMM analysis results of the effect of human impact, vegetation type and the interaction between human impact and vegetation type on different soil properties. If values were transformed prior to analysis, the type of transformation is shown in brackets alongside the name of the property. Conducted using R package 'lmerTest' version 1.0.

Soil property (transformation in brackets)	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
CEC (log10)	(Intercept)	7.87834	0.14757	16.77	53.387	<2e-16 ***
	Human impact	-0.35523	0.22052	34.38	-1.611	0.116
	Vegetation type	-0.28446	0.18379	32.91	-1.548	0.131
	Interaction	0.03694	0.28217	34	0.131	0.897
pH	(Intercept)	8.20E-05	1.98E-05	9.06E+00	4.144	0.00247 **
	Human impact	-1.54E-05	2.52E-05	3.34E+01	-0.612	0.54493
	Vegetation type	1.10E-05	2.08E-05	3.24E+01	0.527	0.60177
	Interaction	6.05E-06	3.22E-05	3.31E+01	0.188	0.85208
15N	(Intercept)	3.7255	0.4644	8.09	8.021	4.03e-05 ***
	Human impact	0.4604	0.6246	33.04	0.737	0.466
	Vegetation type	0.3688	0.5169	31.4	0.714	0.481
	Interaction	1.2015	0.7975	32.6	1.507	0.142
Mn (log10)	(Intercept)	1.60962	0.13683	5.9	11.763	2.55e-05 ***
	Human impact	0.08187	0.14421	32.73	0.568	0.57408
	Vegetation type	-0.0176	0.11858	32.12	-0.148	0.88294
	Interaction	-0.53825	0.18379	32.57	-2.929	0.00617 **
Nt (sqrt)	(Intercept)	33.8743	3.6688	4.58	9.233	0.000393 ***
	Human impact	-3.2857	3.2508	32.37	-1.011	0.319641
	Vegetation type	5.6965	2.6681	31.97	2.135	0.040519 *
	Interaction	-0.5064	4.1409	32.26	-0.122	0.903434
Ca (log10)	(Intercept)	7.1469	0.3521	9.47	20.297	4e-09 ***
	Human impact	-0.214	0.4668	33.41	-0.458	0.64966
	Vegetation type	-1.0812	0.386	32.17	-2.801	0.00855 **
	Interaction	-0.711	0.5959	33.08	-1.193	0.24127
Mg (sqrt)	(Intercept)	22.072	2.762	12.09	7.991	3.63e-06 ***
	Human impact	-7.525	4.008	33.86	-1.878	0.0691 .
	Vegetation type	-10.88	3.332	32.02	-3.266	0.0026 **
	Interaction	5.493	5.124	33.38	1.072	0.2915
K (sqrt)	(Intercept)	8.802	0.7194	5.58	12.235	3.07e-05 ***
	Human impact	-0.527	0.7075	32.72	-0.745	0.462
	Vegetation type	-0.508	0.5813	32.23	-0.874	0.389
	Interaction	-1.1077	0.9015	32.58	-1.229	0.228

Soil property (transformation in brackets)	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
Na (sqrt)	(Intercept)	4.0365	0.4021	8.4	10.038	5.79e-06 ***
	Human impact	-1.2432	0.509	33.22	-2.442	0.0201 *
	Vegetation type	-0.6499	0.4203	32.16	-1.546	0.1318
	Interaction	0.7278	0.6495	32.93	1.121	0.2705
Al	(Intercept)	537.53	188.89	8.81	2.846	0.0196 *
	Human impact	-99.28	249.78	33.26	-0.397	0.6936
	Vegetation type	548.4	206.55	31.94	2.655	0.0123 *
	Interaction	-87.71	318.85	32.9	-0.275	0.785
Fe (log10)	(Intercept)	0.49644	0.14045	15.19	3.534	0.00295 **
	Human impact	-0.08065	0.21171	34.28	-0.381	0.70561
	Vegetation type	-0.0729	0.17662	32.39	-0.413	0.6825
	Interaction	-0.05628	0.27098	33.8	-0.208	0.83671
Mn (log10)	(Intercept)	1.60962	0.13683	5.9	11.763	2.55e-05 ***
	Human impact	0.08187	0.14421	32.73	0.568	0.57408
	Vegetation type	-0.0176	0.11858	32.12	-0.148	0.88294
	Interaction	-0.53825	0.18379	32.57	-2.929	0.00617 **
H (sqrt)	(Intercept)	5.4836	0.9644	7.42	5.686	0.000606 ***
	Human impact	-1.115	1.1472	33.05	-0.972	0.338129
	Vegetation type	0.2673	0.9455	32.2	0.283	0.779164
	Interaction	-0.3398	1.463	32.82	-0.232	0.817782
bases (log10)	(Intercept)	7.5303	0.2972	10.4	25.337	1.09e-10 ***
	Human impact	-0.3467	0.4055	33.58	-0.855	0.39856
	Vegetation type	-0.9937	0.3358	32.22	-2.959	0.00574 **
	Interaction	-0.467	0.5178	33.21	-0.902	0.37364
C:N ratio	(Intercept)	14.2585	0.9443	4.42	15.099	5.73e-05 ***
	Human impact	0.1484	0.7743	32.39	0.192	0.849
	Vegetation type	-0.8538	0.6351	32.06	-1.344	0.188
	Interaction	0.4362	0.9861	32.3	0.442	0.661
Rock content	(Intercept)	0.49397	0.06557	11.14	7.533	1.07e-05 ***
	Human impact	0.02244	0.08844	33.71	0.254	0.801
	Vegetation type	-0.0269	0.0732	32.57	-0.367	0.716
	Interaction	-0.13398	0.11293	33.41	-1.186	0.244
Root biomass (sqrt)	(Intercept)	46.175	6.207	5.13	7.439	0.000617 ***
	Human impact	-11.56	6.156	3.25E+01	-1.878	0.069385 .
	Vegetation type	-2.525	5.058	31.94	-0.499	0.621064
	Interaction	-3.578	7.844	32.33	-0.456	0.651296

Soil property (transformation in brackets)	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
Bulk density (log10)	(Intercept)	-0.52422	0.17122	4.52	-3.062	0.032 *
	Human impact	0.15506	0.1448	32.41	1.071	0.292
	Vegetation type	0.06768	0.1188	32.06	0.57	0.573
	Interaction	-0.07991	0.18443	32.31	-0.433	0.668
Soil mass	(Intercept)	265.123	50.216	7.24	5.28	0.00103 **
	Human impact	-6.769	59.803	32.99	-0.113	0.91057
	Vegetation type	1.416	49.289	32.11	0.029	0.97726
	Interaction	-3.845	76.267	32.75	-0.05	0.9601
Soil depth	(Intercept)	60.236	8.792	5.3	6.852	0.0008 ***
	Human impact	-16.282	8.573	32.6	-1.899	0.0664 .
	Vegetation type	-2.856	7.043	32.1	-0.406	0.6878
	Interaction	2.236	10.923	32.47	0.205	0.8391

Table S16.

Table S16. Values of aboveground tree carbon, Soil Organic carbon (SOC), root carbon and total carbon per m^2 for pristine and disturbed forest and grassland habitats.

Carbon stocks (kg m^{-2})	Value	Pristine forest	Pristine grassland	Disturbed forest	Disturbed grassland
tree carbon	min.	5.053842		4.064274	
	lower quartile	11.95411		7.157122	
	median	16.376322		9.942349	
	upper quartile	20.704421		15.91835	
	max.	33.466236		22.924613	
	mean	17.00212		12.73624	
SOC	min.	10.21096	9.207558	3.55631	10.32657
	lower quartile	10.55713	14.681473	7.727	12.80567
	median	15.26419	21.386348	10.07818	18.86682
	upper quartile	18.37404	26.0696	10.8923	22.44648
	max.	20.06707	32.06703	10.8923	26.23108
	mean	15.0221	20.7681	12.38722	18.10653
root carbon	min.	0.39586	0.3032	0.21268	0.0519
	lower quartile	0.558965	0.5877675	0.42537	0.114595
	median	1.032565	0.904915	0.627745	0.437295
	upper quartile	1.934857	1.4114738	0.92438	0.7003275
	max.	2.686566	2.49354	1.097595	1.41378
	mean	1.284919	1.09256	0.652586	0.495641
total carbon	min.	15.660662	9.510758	7.833264	10.37847
	lower quartile	23.070205	15.2692405	15.309492	12.920265
	median	32.673077	22.291263	20.648274	19.304115
	upper quartile	41.013318	27.4810738	27.73503	23.1468075
	max.	56.219872	34.56057	34.914508	27.64486
	mean	33.3091393	21.8606603	25.7760458	18.6021713

Table S17.

Table S17. LMM analysis results of the effect of human impact, vegetation type and the interaction between human impact and vegetation type on different carbon stocks. If values were transformed prior to analysis, the type of transformation is shown in brackets alongside the name of the property. Conducted using R package 'lmerTest' version 1.0.

Carbon stock (transformation in brackets)	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
Soil Organic Carbon: SOC	(Intercept)	15958.1	2746.12	6.05	5.811	0.0011 **
	Human impact	-1523.72	3077.28	32.67	-0.495	0.6238
	Vegetation type	5235.45	2532.98	31.89	2.067	0.0469 *
	Interaction	-1563.3	3922.99	32.46	-0.398	0.6929
Root Carbon (sqrt)	(Intercept)	1.03251	0.13879	5.13	7.439	0.000617 ***
	Human impact	-0.2585	0.13765	32.48	-1.878	0.069385 .
	Vegetation type	-0.05646	0.1131	31.94	-0.499	0.621062
	Interaction	-0.08001	0.17539	32.33	-0.456	0.651299
Tree Carbon (log10)	(Intercept)	2.4002	0.1944	1.24	12.349	0.03018 *
	Human impact	0.434	0.1483	46	2.926	0.00531 **

Table S18.

Table S18. Estimated values of potential (shaded in grey) and actual carbon stocks in the high elevation area mapped of the Cordillera Urubamba (132,660 km^2; Fig. S1). Values estimated using carbon stock values from pristine and disturbed forest and grassland (Table S16) extrapolated over the areas calculated using landscape mapping (Table S3). 'tree' refers to the aboveground carbon of trees. Values for potential and current overall tree, root and SOC carbon stocks are in bold and shown graphically in Fig. S10.

carbon stocks	area (km2)	min. values of carbon stocks (Gg)	lower quartile values of carbon stocks (Gg)	median values of carbon stocks (Gg)	upper quartile values of carbon stocks (Gg)	max. values of carbon stocks (Gg)	mean carbon stocks (Gg)
potential total tree carbon	**54075.2**	**273.29**	**646.42**	**885.55**	**1119.60**	**1809.69**	**919.39**
potential total root carbon	**76889.7**	**28.32**	**43.64**	**76.48**	**136.83**	**202.17**	**94.41**
potential total SOC	**76889.7**	**762.23**	**905.83**	**1313.33**	**1588.34**	**1816.72**	**1286.14**
potential forest root carbon	54075.2	21.41	30.23	55.84	104.63	145.28	69.48
potential grassland root carbon	22814.5	6.92	13.41	20.65	32.20	56.89	24.93
potential forest SOC	54075.2	552.16	570.88	825.41	993.58	1085.13	812.32
potential grassland SOC	22814.5	210.07	334.95	487.92	594.76	731.59	473.81
potential forest carbon	54075.2	846.85	1247.53	1766.80	2217.80	3040.10	1801.20
potential grassland carbon	22814.5	216.98	348.36	508.56	626.97	788.48	498.74
potential total carbon	76889.7	1063.84	1595.89	2275.37	2844.77	3828.58	2299.94
actual total tree carbon	**6665.2**	**28.07**	**52.48**	**72.67**	**110.86**	**163.29**	**89.14**
actual total root carbon	**76889.7**	**5.35**	**11.21**	**35.49**	**56.65**	**108.63**	**40.04**
actual total SOC	**76889.7**	**755.03**	**954.38**	**1398.31**	**1657.86**	**1926.25**	**1357.83**
actual pristine forest tree carbon	995.2	5.03	11.90	16.30	20.61	33.31	16.92
actual pristine forest root carbon	995.2	0.39	0.56	1.03	1.93	2.67	1.28
actual pristine grassland root carbon	419.9	0.13	0.25	0.38	0.59	1.05	0.46
actual pristine forest SOC	995.2	10.16	10.51	15.19	18.29	19.97	14.95
actual pristine grassland SOC	419.9	3.87	6.16	8.98	10.95	13.46	8.72
actual disturbed forest tree carbon	5670.0	23.04	40.58	56.37	90.26	129.98	72.21
actual disturbed forest root carbon	5670.0	1.21	2.41	3.56	5.24	6.22	3.70
actual disturbed grassland root carbon	69804.6	3.62	8.00	30.53	48.89	98.69	34.60
actual disturbed forest SOC	5670.0	20.16	43.81	57.14	61.76	61.76	70.24
actual disturbed grassland SOC	69804.6	720.84	893.89	1316.99	1566.87	1831.05	1263.92
total actual pristine forest carbon	995.2	15.59	22.96	32.52	40.82	55.95	33.15
total actual pristine grassland carbon	419.9	3.99	6.41	9.36	11.54	14.51	9.18
total actual disturbed forest carbon	5670.0	44.41	86.80	117.07	157.26	197.96	146.15
total actual disturbed grassland carbon	69804.6	724.46	901.89	1347.52	1615.75	1929.74	1298.52
actual total	76889.7	788.46	1018.07	1506.47	1825.37	2198.17	1487.00

Table S19.

Table S19. Estimated values of current carbon stocks for pristine and disturbed habitats given the proportions of forest and grassland vegetation type calculated from landscape mapping (see Table S3).

Habitat	min. values of carbon stocks (kg m^{-2})	lower quartile values of carbon stocks (kg m^{-2})	median values of carbon stocks (kg m^{-2})	upper quartile values of carbon stocks (kg m^{-2})	max. values of carbon stocks (kg m^{-2})	mean carbon stocks (kg m^{-2})
pristine	13.83599	20.75566	29.59279	36.9983	49.79356	29.91238
disturbed	10.18733	13.0997	19.40506	23.49138	28.19081	19.14093

Table S20.

Table S20. LMM analysis results of the differences in climate properties between pristine and disturbed sites. If values were transformed prior to analysis, the type of transformation is shown in brackets alongside the name of the property. Conducted using R package 'lmerTest' version 1.0.

Climate property (transformation, if any, in brackets)	Effect	Estimate	Std. Error	df	t value	Pr(>|t|)
Mean daily temperature (log10)	(Intercept)	1.38653	0.06112	11.771	22.684	4.44e-11***
	Human impact	0.14484	0.08464	10.829	1.711	0.115
Mean daily minimum temperature	(Intercept)	0.7128	0.3966	12.505	1.797	0.0965.
	Human impact	0.1539	0.4745	11.015	0.324	0.7518
Mean daily maximum temperature	(Intercept)	9.832	1.761	10.152	5.582	0.000221***
	Human impact	1.938	2.276	5.054	0.851	0.433009
Absolute minimum temperature	(Intercept)	-4.028	1.525	17	-2.641	0.0171*
	Human impact	-1.447	2.10E+00	17	-0.688	0.5006
Absolute maximum temperature (log10)	(Intercept)	3.0305	0.1245	13.04	24.351	2.95e-12***
	Human impact	0.1302	0.1601	10.299	0.813	0.435
Mean daily temperature variation (log10)	(Intercept)	2.1155	0.1482	12.37	14.277	4.71e-09***
	Human impact	0.1434	0.189	9.627	0.759	0.466
Absolute max. daily temperature variation (log10)	(Intercept)	3.033	0.1446	17	20.98	1.37e-13***
	Human impact	0.1565	0.1993	17	0.786	0.443
Days yr where max. temperature does not reach 5øC (log10)	(Intercept)	3.0486	0.4126	13.742	7.389	3.81e-06***
	Human impact	-0.5616	0.5633	7.15	-0.997	0.351
Days yr where temperature dropped equal or below 0øC	(Intercept)	152.78	32.63	17	4.683	0.000214***
	Human impact	-27.28	44.97	17	-0.607	0.552161
Mean daily relative humidity	(Intercept)	88.027	2.155	10.234	40.85	1.13e-12***
	Human impact	-2.358	2.204	6.844	-1.07	0.321
Days yr where relative humidity passed 90%	(Intercept)	280.67	19.32	17	14.525	5.15e-11***
	Human impact	-10.17	26.64	17	-0.382	0.707
Days yr with fog occurrence (relative humidity passed 99%)	(Intercept)	203	16	17	12.686	4.28e-10***
	Human impact	-23.5	22.06	17	-1.065	0.302
Absolute minimum relative humidity (log10)	(Intercept)	3.0077	0.2484	12.689	12.109	2.43e-08***
	Human impact	-0.3797	0.324	6.117	-1.172	0.285

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Chapter 4

Elevational patterns of *Polylepis* tree height (Rosaceae) in the high Andes of Peru: role of human impact and climatic conditions.

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Elevational patterns of *Polylepis* tree height (Rosaceae) in the high Andes of Peru: role of human impact and climatic conditions

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We studied tree height in stands of high-Andean *Polylepis* forests in two cordilleras near Cuzco (Peru) with respect to variations in human impact and climatic conditions, and compared air and soil temperatures between qualitatively defined dry and humid slopes. We studied 46 forest plots of 100 m^2 of five *Polylepis* species at 3560–4680 m. We measured diameter at breast height (dbh) and tree height in the stands (1229 trees in total), as well as air and soil temperatures in a subset of plots. The data was analyzed combining plots of given species from different sites at the same elevation (±100 m). There was no elevational decrease of mean maximum tree height across the entire data set. On humid slopes, tree height decreased continuously with elevation, whereas on dry slopes it peaked at middle elevations. With mean maximum tree heights of 9 m at 4530 m on the humid slopes and of 13 m at 4650 m on the dry slopes, we here document the tallest high-elevation forests found so far worldwide. These highest stands grow under cold mean growing season air temperatures (3.6 and 3.8°C on humid vs. dry slopes) and mean growing season soil temperatures (5.1 vs. 4.6°C). Mean annual air and soil temperature both decreased with elevation. Dry slopes had higher mean and maximum growing season air temperatures than humid slopes. Mean annual soil temperatures did not significantly differ and mean annual air temperatures only slightly differed between slopes. However, maximum air temperatures differed on average by 6.6 K between dry and humid slopes. This suggests that the differences in tree height between the two slopes are most likely due to differences in solar radiation as reflected by maximum air temperatures. Our study furthermore provides evidence that alpine *Polylepis* treelines grow under lower temperature conditions than global high-elevation treelines on average, suggesting that *Polylepis* species may have evolved special physiological adaptations to low temperatures.

Keywords: air temperatures, forest structure, soil temperatures, solar radiation, alpine treeline, tropical forest

INTRODUCTION

The tropical Andes support some of the World's highest forests, mainly formed by species of the genus *Polylepis* (Rosaceae). With about 30 species (Kessler and Schmidt-Lebuhn, 2006), this tree genus has radiated into a wide range of ecological niches, ranging from very wet cloud forests to high-elevation semideserts (Simpson, 1986; Schmidt-Lebuhn et al., 2010). Two features have rendered *Polylepis* prominent in the literature of tropical high mountain ecosystems. First, *Polylepis* forms one of the highest alpine treelines worldwide, with 3 m tall trees recorded at 4810 m on Volcán Sajama in Bolivia (Hoch and Körner, 2005), only surpassed by similarly tall *Juniperus tibetica* at 4900 m in Tibet (Miehe et al., 2007). Second, in much of the tropical Andes, the distribution of *Polylepis* forests is disconnected from that of other montane forests at lower elevations. Accordingly, the upper limit of the closed montane forest belt found at elevations between 3200 and 3800 m is often considered to represent the natural alpine treeline (Gosling et al., 2009; Urrego et al., 2011), while it remains debated to what degree the disjunct and patchy distribution of *Polylepis* forests, with stands often being restricted to special microsites, is natural or man-made (e.g., Kessler, 2002; Gosling et al., 2009; Urrego et al., 2011; Gareca et al., 2013). Nevertheless, there is no doubt that many *Polylepis* forest stands are currently strongly affected by human activities, either directly by timber extraction, or indirectly by cattle grazing and associated grassland burning (Kessler, 2000, 2002; Renison et al., 2006, 2010). It has been shown that these activities influence forest density and height (Toivonen et al., 2011), tree regeneration (Cierjacks et al., 2007; Bader and Ruijten, 2008), and the genetic constitution of *Polylepis* populations (Hensen et al., 2012; Gareca et al., 2013). In this context, understanding how climatic conditions, as well as human activities, affect the growth of *Polylepis* trees is of considerable interest, both with regard to the ecology of high-elevation forest

ecosystems, and as a baseline for the management of natural tree resources.

Tree height is one of the most meaningful ecological variables regarding the growth performance of trees, yet its spatial variability remains incompletely documented and understood, both for the tree growth form in general (Cramer, 2012) and for *Polylepis* trees in particular (Kessler et al., 2007). While it is well known that, in general terms, tree height decreases with decreasing temperatures, water availability, and nutrient availability, these relationships are not necessarily linear and may also differ between taxa and geographical regions. In mountains, tree height generally decreases with increasing elevation (e.g., Wilson et al., 1987; Young, 1993; Kessler et al., 2007), but, especially near the upper (alpine) treeline, a wide range of tree height-elevation relationships can be found (Holtmeier, 2009; Körner, 2012). Some studies have documented linear decreases with elevation (e.g., Paulsen et al., 2000; Kessler et al., 2007), while others have found increasingly steep declines in tree height close to treeline elevation (e.g., Barrera et al., 2000; Hertel and Wesche, 2008; Hertel and Schöling, 2011b) or even abrupt treelines (e.g., Miehe et al., 2007). Furthermore, treelines may be formed by closed stands of trees or by increasingly scattered tree individuals (Miehe et al., 2007; for a review of treeline physiognomy see Holtmeier, 2009). These different treeline forms may, among other factors and depending on spatial scale, be caused by natural factors such as topography, water availability, and disturbance history as well as by human impact (Holtmeier, 2009; Quesada et al., 2009; Harsch and Bader, 2011; Cramer, 2012).

The relationship of humidity and elevation in influencing tree growth is also complex, since the precipitation regime does not necessarily show a linear elevational pattern, but is intimately dependent on the elevational position of the cloud base and the available source of water (Barry, 1992). While, generally speaking, tree height increases with increasing water availability (except in water-saturated soils; Koch et al., 2004; Oldham et al., 2010), in high mountains this effect may be overridden by low temperatures. Thus, trees may grow taller on warm, sunny slopes than on cold, shady ones even if the latter are more humid (Kessler et al., 2007; Holtmeier, 2009; Paulsen and Körner, 2014). For example, *Polylepis tarapacana* forests, at the aridity limit of genus in the high Andes of southwestern Bolivia, do not grow on the more humid but less sunny southern slopes, and instead are restricted to the dryer and more sunny northern ones (Kessler, 1995b; Kessler et al., 2007).

A further challenge in exploring structural forest parameters at treeline elevations is that human impact has affected treelines worldwide via timber extraction, burning and use as grazing lands for domestic animals (Laegaard, 1992; Kessler, 1995b, 2000; Hemp, 2005; Toivonen et al., 2011; Schüler et al., 2012). Human impact can often be detected in structural parameters of forest stands, such as by a lack of saturation of tree height with increasing stem diameter, i.e., a lack of decreasing tree slenderness. In mature, natural forests, the tree height-dbh (diameter at breast height) relationship usually shows a saturation effect because tree height is limited by ecological factors such as water and nutrient availability, or the lack of adequate thermal conditions (Anfodillo et al., 2012; Lines et al., 2012; Marshall et al., 2012). Trees that have reached this potential maximum height cannot grow any taller but, as they increase in age, they continue to form new annual growth rings, thus increasing in diameter (Domic and Capriles, 2009). By contrast, in disturbed forests where especially large trees are extracted, no such saturation is visible in the remaining tree cover.

The functional causes determining the decrease of tree height with elevation, as well as the upper limit of tree growth, are still debated (see, e.g., contradictory opinions stated by Miehe et al., 2007; Holtmeier, 2009; Körner, 2012). There is no question that, leaving aside specific local conditions, the location of the upper treeline is closely linked to low temperatures. In their global reviews of treeline positions, Körner and Paulsen (2004) and Paulsen and Körner (2014) found that the mean soil temperature of the growing season, defined by them as the period with soil temperatures at 10 cm depth consistently above 3.2°C, averages 6.4–6.7°C at alpine treeline positions worldwide, and can be used to infer mean air temperatures. Although some of the tropical sites included in their studies had somewhat lower values (4.5–5.6°C), on-site measurements at Andean sites suggest that values could even be in the range of 3–4°C (Kessler and Hohnwald, 1998; Bendix and Rafiqpoor, 2001; Hoch and Körner, 2005; Hertel and Wesche, 2008). However, since these were mostly short-term measurements, their validity remains to be confirmed. It also remains unclear how these low temperatures physiologically limit tree growth, and whether low soil or air temperatures are decisive for treeline formation. Hampered tree growth at high elevations may be related to both temperature minima (e.g., lethal frost) or maxima (via annual thermal sum). Physiologically, tree growth may be limited, e.g., by thermal constraints in tissue formation due to the strong aerodynamic coupling of trees to the atmosphere (e.g., Wilson et al., 1987; Körner, 2012) or limited water and nutrient uptake by the fine root system (Leuschner et al., 2007; Hertel et al., 2008; Hertel and Schöling, 2011a).

In the present study, our aim was to study elevational patterns of tree height among five species of *Polylepis* in relation to human impact and climatic conditions in the Cordilleras Vilcanota and Vilcabamba, Cuzco, Peru. We tested the following specific hypotheses:

(1) Tree height is lower in elevation belts where forest stands are affected by humans, compared to elevation belts where the stands are in natural conditions.
(2) Tree height is lower on humid slopes than on drier slopes because of cloudiness and decreased solar radiation and thus lower temperatures.

MATERIALS AND METHODS

STUDY AREA

We carried out the field work in the Cordilleras Vilcanota and Vilcabamba, Cuzco, Peru (13°07'–13°17' S and 72°02'–72°29' W) for seven years between 2006 and 2012 (**Figure 1**). The Cordilleras Vilcanota and Vilcabamba are known to support some fairly extensive, and partly well preserved *Polylepis* forests at elevations between 3300 and 4950 m (Lloyd and Marsden, 2011; Toivonen et al., 2011). The climate of the region varies from humid to semi-arid with a clear wet season from November to

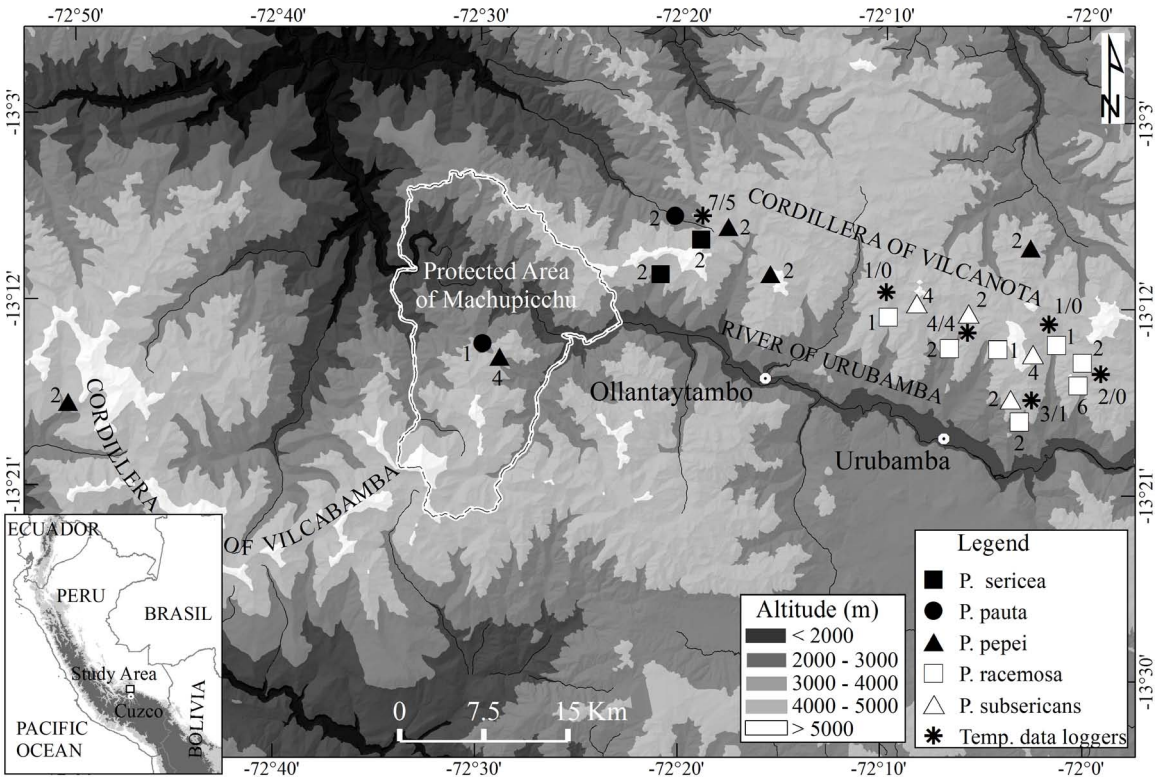

FIGURE 1 | Map of the study region, showing the location of the study sites and the temperature data loggers. The number of plots and temperature data loggers (air/soil) in each site is indicated next to the symbols.

April. Diurnal temperature fluctuations are pronounced, especially in the dry season. There is a strong geographical gradient in precipitation across the study area, caused by specific orography directing winds and cloud movements. This is shown by the contrasting precipitation records at the climate stations of Urubamba (2863 m), with 454 mm mean annual precipitation, and Wiñaywayna, protected area of Machupicchu (2800 m), with 1606 mm (records of former INRENA, National Institute of Natural Resources of Peru and SENAMHI, National Service of Meteorology and Hydrology of Peru). Based on this strong precipitation gradient and, consequently, strikingly different vegetation composition, we separated the studied sites as either dry or humid ones. The separation was mostly qualitative and the *Polylepis* species found at the different sites were used as a first indicator of the prevalent humidity conditions based on the known ecological distribution of the species (according to e.g., Kessler, 1995a,b, Fjeldså and Kessler, 1996). On the humid sites, *Polylepis* trees were covered in mats of epiphytic bryophytes, whereas on the dry sites there were noticeably less bryophytes. Moreover, as an indication of drought, the low elevation stands on dry sites are intermixed with drought-deciduous trees. The climate data from the lower elevation climate stations supports our qualitative classification.

The study sites of humid and dry areas were located on the same soil type, Regosol, according to classification of Food and Agriculture Organization of the United Nations (IMA, Instituto de Manejo de Agua y Medio Ambiente, Gobierno Regional de Cuzco, Peru, 2014). Regosols are very weakly developed mineral soils found in eroding lands, in particular in arid and semi-arid areas and in mountain regions.

In total, five *Polylepis* species are found in our study area, being segregated by elevation and humidity (Toivonen et al., 2011). Forest stands are mostly monospecific with *P. pauta* Hieron., *P. sericea* Wedd. and *P. pepei* Simpson being found in humid areas while *P. racemosa* Ruiz & Pav. and *P. subsericans* Macbr. are found in drier areas. Species have some specific climatic adaptations in their functional traits, with high-elevation species, for example, having smaller leaves and higher root tip abundance compared with lower elevation species (Toivonen et al., 2013).

The study region has been used by humans for millenia (Mosblech et al., 2012) and *Polylepis* forests, at present, are subject to different degrees of human impact (Toivonen et al., 2011). This region is, thus, ideal to study elevational trends of tree height under differing patterns of humidity and human impact.

FIELD SAMPLING

Sampling was aimed at covering the widest possible elevational range of *Polylepis* stands while being largely determined by the availability of forest patches. In total, we studied 46 plots in *Polylepis* stands, ranging from 3560 to 4680 m, located in varying expositions. Because of the scattered distribution of forest stands, it was often impossible to find replicated, suitable forest

sites at specific elevations. We, therefore, combined plots of a given species from different sites at the same elevation within elevational belts of 200 m (i.e., a deviation in elevation of ±100 m), reasoning that within-belt elevational differences are minor compared to the overall elevational gradient that we covered (3560–4680 m; **Table 1**). In total, we studied six elevational belts in humid and six in dry areas. Within each elevational belt, we established 3–6 plots of 10 m × 10 m each, with the exception of one belt where only a single suitable plot site could be located. Plots were located as far as possible in the center of the forest stands, at least 25 m from the forest edge to give a representative sample of the structure of the forest stand.

In each plot we measured dbh and visually estimated tree height of all trees ≥10 cm of circumference at breast height. For tree height estimation, we used a 1.5 m long measuring stick placed next to each tree. The visual tree height estimation was tested for its accuracy in particular in case of taller trees by comparing the results with a standard stick method (i.e., by calculating tree height from the distance of the researcher to a stick of known height and the distance to the tree stem base according to the mathematical second intercept theorems). The results of the two methods were reasonably similar (with a maximum divergence of the results of both methods ±50 cm). We ended up by using the estimation method, because it was much more feasible to use in topographically demanding terrain. Furthermore, since the height of the trees was relatively low overall (in comparison, e.g., to mature lowland forest trees), we are rather confident that the estimates are sufficiently accurate. Because human impact is known to significantly affect *Polylepis* forest structure both in the study region (Toivonen et al., 2011) and elsewhere (Renison et al., 2006), we recorded signs of impact of human land use (cut trees, trails, fire scars) and of the domestic animals (tracks, feces, signs of grazing).

In total, we measured 1229 tree individuals of the five species of *Polylepis* (**Table 1**). The number of tree individuals measured per elevational belt varied from 52 to 164 (mean 102.4 ± 30.1 SD). Forest stands with signs of human impact (e.g., footpaths, cut trees, charcoal, feces of domestic animals, etc.) were regarded as potentially anthropogenically influenced whereas stands without such signs were regarded as not significantly affected by humans (thus representing the potential performance of the trees under natural growth conditions). In six of the elevational belts, we recorded signs of human influence whereas the other six belts were considered to be unaffected by humans (**Table 1**).

MICROCLIMATIC MEASUREMENTS

We measured air temperature in the shaded canopy with data-loggers (DS1922 Thermochon iButtons, Hubbart et al., 2005) in 18 of our study plots and within the soil in the shaded root zone (10 cm depth) in 10 plots (**Figure 1**). Measurements were run for one, two or three years (between June 2006 and April 2012) in each plot depending on the accessibility of the stand. However, due to the problematic access, the measurements from the uppermost stands covered only the period between begin of July to end of May. However, during the whole measurement period (2006–2009) inter-annual variations in temperature were small. So in cases, where we had data from 2 to 3 years per site (most plots), we

Table 1 | Characteristics of the elevation belts and number of temperature data loggers in each belt.

Species	Mean elevation (m)	Elevation range (m)	No. of plots	Human impact	No. of individuals	Mean maximum tree height (m)[1]	No. of temperature data loggers (air/soil)
Humid slope							
P. pauta	3730	3560–3760	3	No	52	14.3	2/1
P. sericea	3790	3725–3910	3	Yes	84	8.4	1/1
P. pepei	4140	4120–4195	3	Yes	108	5.8	1/1
P. sericea	4230	4230–4230	1	Yes	94	4.2	1/1
P. pepei	4370	4235–4415	6	No	164	9.2	2/1
P. pepei	4530	4440–4565	3	No	107	8.7	0/0
Dry slope							
P. racemosa	3980	3865–4070	5	No	96	15.9	2/2
P. racemosa	4160	4140–4230	4	Yes	103	9.6	3/1
P. racemosa	4300	4280–4355	4	No	76	18.5	1/0
P. subsericans	4340	4270–4390	5	Yes	105	11	1/1
P. subsericans	4430	4410–4460	4	Yes	90	11.3	3/1
P. subsericans	4650	4635–4680	5	No	150	12.8	1/0

Human impact was determined based on signs of humans (paths, cut trees, and branches) or their animals (hoofprints, feces).
[1] *Mean of 10% tallest trees.*

used the mean values. Measurement readings were mostly taken at 4 h intervals (starting at 00:00). In three sites, air temperature was recorded in 2 h intervals to assess whether we recorded daily minima and maxima with 4 h measuring interval at the other sites (**Table 1**). Growing season length was defined as the number of days where soil temperature at 10 cm depth is continuously above 3.2°C (Körner and Paulsen, 2004).

DATA ANALYSES

We quantified mean maximum tree height in each elevational belt by averaging the height of 10% of the tallest trees in each belt. The relationship between mean maximum tree height and elevation was analyzed using linear regression, based on mean values per elevational belt. We tested statistically the differences in mean maximum tree height in natural stands within each slope.

In each elevational belt, we plotted tree height of each individual tree (≥10 cm of circumference at breast height) against dbh and fitted both a linear and a logarithmic function to the data points. Models were compared via their R^2 and AICc-values (models with a delta AICc > 4 were claimed to be substantially better following Burnham and Anderson, 2002). As an additional potential measure of saturation of tree height, we calculated slenderness of each tree by dividing tree height by dbh (Wang et al., 1998) and compared the values between elevational belts via Analysis of Variance.

We compared temperature values between the humid and dry slopes with a *t*-test. For the temperature variables that showed a significant linear relationship with elevation, the residuals of linear regression with elevation were compared. Temperature data from both slopes were combined to extract a common trend in a decrease of temperature with elevation. The data was combined, because we did not have any *a priori* reason to expect a decrease in temperature by increasing elevation to be different between the slopes. If there was a significant trend in temperature decrease with elevation, a residual variation of temperature was compared between the slopes. If there was not a significant elevational trend in temperature, raw values were compared. In this way, the effect of elevation was taken into account before comparing the temperature conditions between the slopes, because the measurements came from different elevations. All analyses were performed with (R Core Team, 2012) and package qpcR (Spiess, 2012).

RESULTS

TREE HEIGHT VERSUS HUMAN IMPACT AND HUMIDITY

Analysing all twelve elevational belts together, there was essentially no elevational trend in mean maximum tree height ($R = -0.06$, $p = 0.85$). The expected negative relationship was slightly more evident, but still not significantly, when belts affected by human activities ($R = -0.32$, $p = 0.54$) were analyzed separately from those without human impact ($R = -0.44$, $p = 0.38$). Also, there were no significant elevational declines of tree height either when slopes were analyzed separately (dry slope: $R = -0.19$, $p = 0.51$; humid slope: $R = -0.59$, $p = 0.22$). Plotting mean maximum tree height against elevation showed several distinct patterns (**Figure 2A**). First, trees on the dry slope were generally considerably taller than trees at the same elevation on the wet slope ($p < 0.05$). Second, tree height at anthropogenically disturbed elevational belts was noticeably (but only marginally significantly) lower than at undisturbed elevational belts ($p = 0.055$). Third, undisturbed belts on the humid slope showed a continuous decrease of mean maximum tree height with elevation whereas on the dry slope tree height peaked at mid-elevations. This decrease in tree height was also supported by our observation of other patches of remnant vegetation without *Polylepis* at even lower elevations in the Urubamba valley (M. Kessler et al., personal observation).

Tree height and dbh were moderately to highly correlated with each other in all elevational belts, but the shapes of the relationships varied (**Figure 3**). In four belts (*pauta* 3730 m, *racemosa* 3980 and 4300 m, *subsericans* 4650 m), all of which had no signs of human impact, tree height showed a distinct saturation with increasing dbh so that the R^2 values of the non-linear models were at least 0.1 higher than those of the corresponding linear models, with ΔAICc values > 19. The other belts, including two undisturbed and all six disturbed belts, showed more or less linear relationships with ΔR^2 values between 0.00 and 0.09 and ΔAICc values between 1 and 23.

Slenderness was significantly higher at the two belts of *P. sericea* than at the other localities (one-way ANOVA, $F_{12,1404} = 11.033$, $p < 0.001$), but there were no elevational trends (linear regressions, humid slope: $R^2 = 0.21$, $p = 0.35$; dry slope: $R^2 = 0.00$, $p = 0.96$), nor were there visible differences between disturbed and undisturbed belts.

TEMPERATURE CONDITIONS ON HUMID AND DRY SLOPES

Overall, most temperature variables showed a decrease with elevation, with mean annual air temperature decreasing at a rate of 4.2 K per 1000 m of elevational increase on the humid slope and 4.7 K on the dry slopes (**Figure 4**). Mean air temperature of the growing season showed a steeper elevational decline both on the dry (5.5 K per 1000 m) and on the humid slope (4.3 K per 1000 m). Mean annual soil temperatures (combined for both slopes) declined at a rate of 3.9 K per 1000 m, absolute minimum temperatures at 3.5 K per 1000 m, absolute maximum temperatures at 3.0 K per 1000 m, and mean temperatures of the growing season at 2.8 K per 1000 m. Absolute maximum and minimum air temperatures showed no clear elevational patterns.

Considering temperature conditions at the highest sites, on the humid slope at 4330 m we measured a mean annual air temperature of 3.3°C and a mean annual soil temperature of 4.7°C, with mean air and soil temperatures for the growing season (310 days) 3.6 and 5.1°C, respectively. On the dry slope at 4450 m, mean annual air and soil temperatures were 3.3 and 4.0°C, respectively, while mean air and soil temperatures for the growing season (232 days) were 3.8 and 4.6°C, respectively (**Figure 5**). Days on which air temperature was >5°C were 34 days for dry and 36 days for humid sites. Annual thermal sums based on air temperatures were also rather similar between dry and humid sites (1124°C in dry and 1181°C in humid sites), as were annual mean air temperatures (3.3°C). Annual thermal sums based on soil temperature differed between dry and humid sites (1293°C in dry and 1502°C in humid areas, however, note that these numbers covered only a c. 11 months-long period of measurements). The definition of

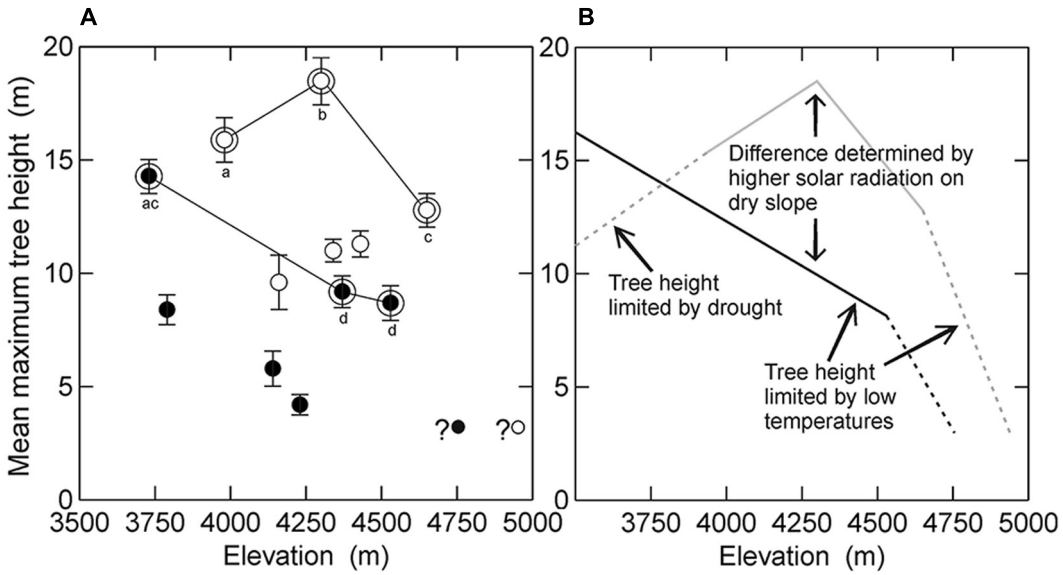

FIGURE 2 | Relationship of mean maximum tree height to elevation in the study region. (A) Visualization of the data from this study, distinguishing between the dry (white symbols) and humid (black symbols) slopes as well as sites without evidence of human impact (double symbols linked by lines) and those with human impact (single symbols). Whiskers indicate standard deviations of the means. The two small symbols with question marks in the lower right corner correspond to the putative highest forest stands identified from aerial photographs of the study region (Toivonen et al., submitted manuscript). Different letter indicate statistically significant differences in mean maximum tree height between sites without human impact (*U* test after Mann & Whitney, $p < 0.05$). **(B)** Schematic representation of the natural pattern of tree height in the study region and the environmental factors associated with it, contrasting the dry (gray line) and humid (black line) slopes. Dashed lines correspond to expected tree height-elevation relationships based on indirect evidence (see text for details).

growing season as the number of days where soil temperature at 10 cm depth is continuously above 3.2°C (Körner and Paulsen, 2004) appeared to reflect a threshold of 0°C in daily minimum, but not daily mean air temperature (**Figure 5**).

Contrasting the temperature values of the humid and dry slopes, we found significant differences for absolute maximum air temperature and for mean air temperature of the growing season. There was also a tendency toward higher mean annual air temperatures on the dry slope, but this was only marginally significant. Mean annual soil temperatures did not differ between dry and humid slopes (**Table 2**).

DISCUSSION

TREE HEIGHT AND HUMAN IMPACT

At six of the elevational belts studied, we found no evidence of human impact whilst six other belts showed signs of human influence (footpaths, cut trees, charcoal and/or feces of domestic animals). Elevational belts with prevalent human activity did not show a saturation of tree height with increasing dbh. The height-dbh relationship was closer to linear in disturbed elevational belts, whereas at four of the undisturbed elevational belts, maximum tree height leveled off at a certain dbh. While very little is known about tree height-dbh relationships at high elevations, we interpret a tree height saturation with dbh as an indication of a natural tree growth pattern, where trees have reached their ecologically determined potential tree height at a given elevation (Anfodillo et al., 2012; Lines et al., 2012; Marshall et al., 2012).

Deviations from this general pattern were found at three belts dominated by *Polylepis pepei*, a relatively small species originally described as a shrub (Simpson, 1979) or tree to 3 m tall (Kessler, 1995a). Since then, a study at 3800–4050 m in Bolivia has documented trees of *P. pepei* of about 8 m height and 23 cm dbh (Hertel and Wesche, 2008) and the mean maximum tree height of 9.2 m and dbh values of up to 35.7 cm documented here at 4370–4530 m further validate that this species can become larger than previously believed. Yet, two elevational belts did not show tree height saturation despite being stands in extremely remote locations without signs of human impact and therefore regarded by us as truly undisturbed. It thus appears that *P. pepei* does not achieve a significant increase in dbh once maximum tree height has been reached, perhaps suggesting that these trees do not reach great ages. In fact, the oldest documented *P. pepei* trees are only 137 years old (Roig et al., 2001; Jomelli et al., 2012), whereas more than 700 years old *P. tarapacana* trees have been found in Bolivia (Solíz et al., 2009).

Another interesting case is presented by the stands of *P. pepei* studied in the elevational belt at 4140 m. Here, trees showed a clear height saturation, yet, with a mean maximum height of 5.8 m, were considerably lower than the stands higher up at 4370 and 4530 m, which were around 9 m tall. We believe that this is due to the fact that, at 4140 m, where human impact was fairly pronounced, the stands were restricted to very steep, rocky slopes with shallow soils on which trees could only develop stunted growth forms. Thus, although these trees apparently

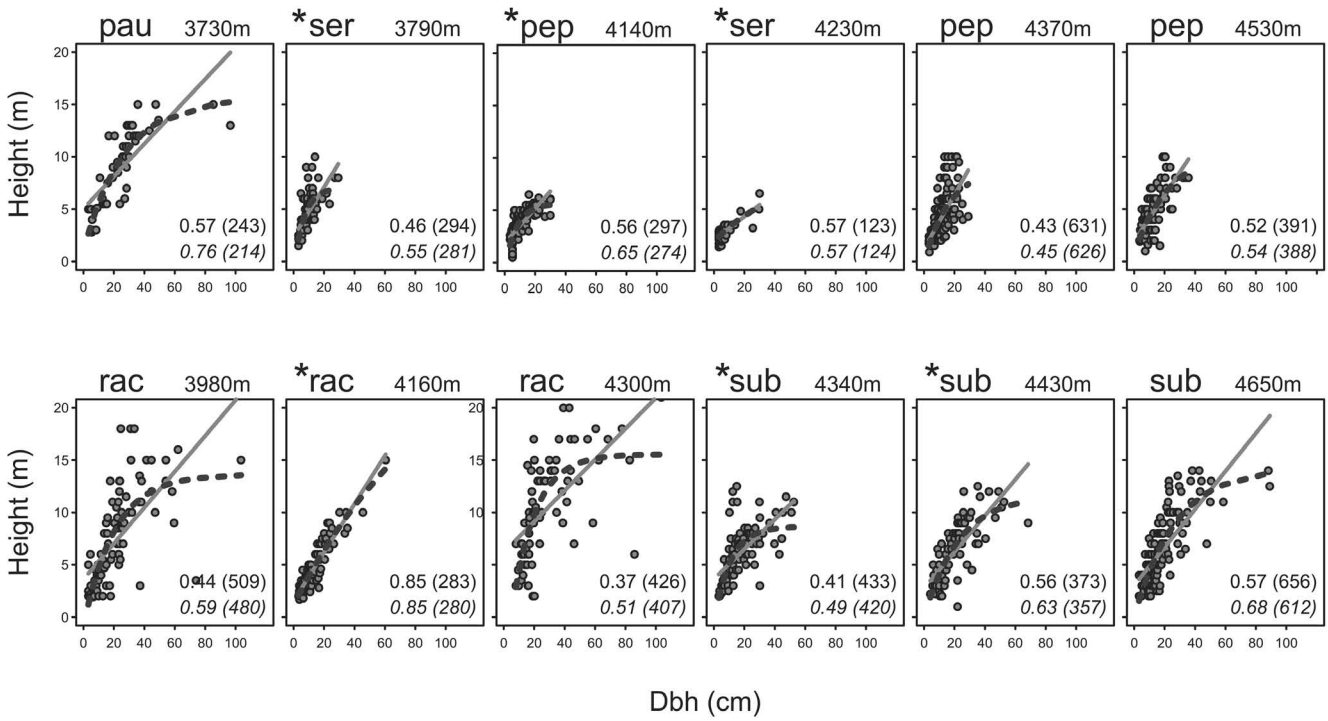

FIGURE 3 | Height-dbh relationships of *Polylepis* trees of five species at different elevational belts at the humid (upper row) and dry (lower row) sites of the Cordilleras Vilcabamba and Vilcanota. Belts in which the studied forest stands had signs of human impact are marked by asterisks. Elevation indicates mean elevation of the plots in each elevational belt. Numbers are R^2 values followed by AICc values in brackets, above for the linear models (continuous lines) and below in italics for the non-linear models (dashed lines). Species name abbreviations: pau, *pauta*; pep, *pepei*; rac, *racemosa*; ser, *sericea*; sub, *subsericans*.

reached their full potential under these site conditions, their height was presumably not representative for the elevational belt as such.

ELEVATIONAL PATTERNS OF TREE HEIGHT IN NATURAL STANDS

The highest stands studied were located at 4570 m on the humid slopes and at 4680 m on the dry slopes, but based on aerial photographs, stands of *P. pepei* on the humid slope are found at about 4700 m and of *P. subsericans* on the dry slope at 4950 m (**Figure 2A**). Although the aerial photographs do not allow us to quantify tree height, if we consider that these are the highest stands in the study region, these trees are unlikely to be more than a few meters tall. This suggests that tree height must decrease fairly abruptly above the stands found by us. This apparent abrupt decrease contradicts the simple height-elevation models applied to Bolivian *Polylepis* forests by Kessler et al. (2007) but is in accordance with height measurements of *Polylepis pepei* stands in Bolivia (Hertel and Wesche, 2008) and of other tree species at tropical treelines elsewhere (Miehe and Miehe, 1994; Miehe et al., 2007).

On the humid slope, mean maximum tree height decreased in undisturbed stands gradually from 14 m at 3730 to 9 m at 4530 m (**Figure 2A**). This constant decrease of tree height with elevation is the most commonly observed pattern of tree height-elevation relationships (e.g., Young, 1993; Paulsen et al., 2000; Kessler et al., 2007), although we cannot extrapolate this beyond the elevations studied by us. Yet, our observations in the study region also show that tree height further increases below 3700 m in mixed species forests that lack *Polylepis* trees (**Figure 2B**, M. Kessler, unpublished data). In contrast, in undisturbed stands on the dry slopes, tree height peaked at 18.5 m at 4300 m and decreased toward both lower elevations (16 m at 3980 m) and higher elevations (13 m at 4650 m).

We are thus faced with marked differences in tree height-elevation relationships on the climatically contrasting slopes of our study region, both in terms of pattern and magnitude. The hump-shaped pattern of tree height on the dry slope is difficult to interpret, but one possible explanation can be drought stress toward the valley bottom (e.g., mean annual precipitation 454 mm in Urubamba, following the Peruvian climate service SENAMHI, registration period 1963–1998). While natural vegetation is largely absent from this valley that has been under intensive cultivation for millennia, and tree height can thus not be measured below the elevations covered by us, vegetation remnants suggest that, below the lower limit of *P. racemosa* at about 3500 m, the original vegetation may have consisted of a low stature forest of *Acacia* and *Prosopis* (W. Galiano, personal communication). This thus represents an even more pronounced reduction of tree height with decreasing elevation (**Figure 2B**). Such drought-related inverse treelines have been documented, e.g., at the forest-steppe ecotone in Patagonia (Hertel et al., 2008) and are also common in rain-shadowed mountain valleys (Holtmeier, 2009). However, it is

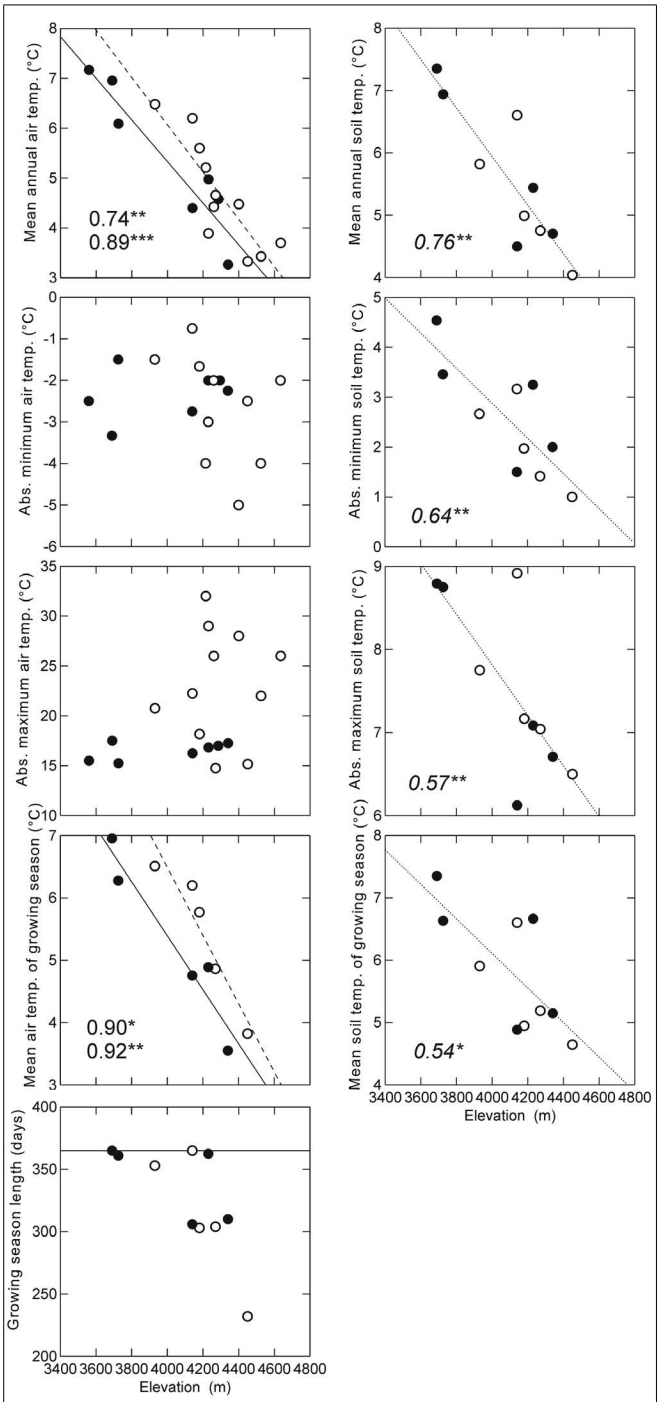

FIGURE 4 | Relationships of measured climatic variables to elevation along the dry (open symbols, dashed lines) and humid (closed symbols, continuous lines) slopes. Growing season length was defined as the number of days with soil temperatures at 10 cm depth consistently above 3.2°C following Körner and Paulsen (2004). Lines show significant linear regression trend lines, numbers indicate the R^2 values of the regression analyses (top: dry slope; bottom: humid slope). For soil temperatures, regression lines were drawn and calculated combining data from both slopes. In the graph of the growing season length, the horizontal line represents the maximum possible number of days (365) $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

also possible that mean maximum tree height at the lowest elevation belt on dry slopes is influenced by a long-term human impact, even though we did not find recent signs of human activities in the studied stands.

At higher elevations, the marked differences in mean maximum tree height on the humid and dry slopes also begs explanation. It is well known that trees grow taller under semi-arid to subhumid mountain conditions than in wet habitats (Kessler et al., 2007; Miehe et al., 2007; Körner, 2012; Paulsen and Körner, 2014), so that these differences are most likely a result of climatic factors such as lower solar radiation and temperatures under cloudy conditions (Lauer, 1982). Among the temperature values measured by us, we only found significant differences between the dry and humid slopes with respect to maximum and mean air temperatures. Mean air temperatures were less than 1 K higher at a given elevation on the dry than on the humid slope, whereas maximum air temperatures differed on average by 6.6 K between dry and humid slopes. Therefore, it seems that the differences in tree height between the two slopes are most likely due to differences in solar radiation as reflected by maximum air temperatures. While our measurements of within-canopy air temperatures can only be taken as rough indications of the actual temperature of the foliage, our results nevertheless show that tree height in the study region is more closely related to air and presumably above-ground tissue temperatures than to soil temperatures, which did not differ markedly between dry and humid slopes. Aspect- and, hence, radiation-related differences in tree height have also previously been documented in *Polylepis* forests in Bolivia (Kessler et al., 2007). Further, it has been shown that maximum photosynthesis, and therefore possibly tree growth, is limited by cloud cover in Amazonian cloud forest trees, emphasizing the importance of solar radiation on tree growth (Letts and Mulligan, 2005). However, a negative effect of solar radiation on biomass production has also been documented in humid cloud forests with trees investing more in biomass production in the cooler season with lower solar radiation and more in maintenance during the warmer and high solar radiation period (Girardin et al., 2014).

Comparisons of the annual mean and maximum temperatures between the sites where temperatures were recorded in 2 h intervals (one site on the humid and one on the dry slopes) and sites where temperatures were recorded in 4 h intervals, showed that, specifically on dry slopes, logging interval may have affected daily air temperature maxima, with lower values being registered for 4h interval recordings in comparison with 2 h interval recordings. This means that real values for annual mean and maximum air temperatures on the dry slopes would be higher than we measured. On the humid slope, the difference in the air temperatures between the measurement carried out in 2 and 4 h intervals was marginal ($<$0.5 K). However, even with this possible measurement error, the overall differences in air temperatures between the slopes, with dry slopes being warmer than humid slopes, our results provide support for the role of air temperatures in explaining the difference in tree height between dry and humid slopes.

Although most of our interpretation of differences in tree height between the dry and humid slopes focuses on climatic differences, it should be borne in mind that other factors may

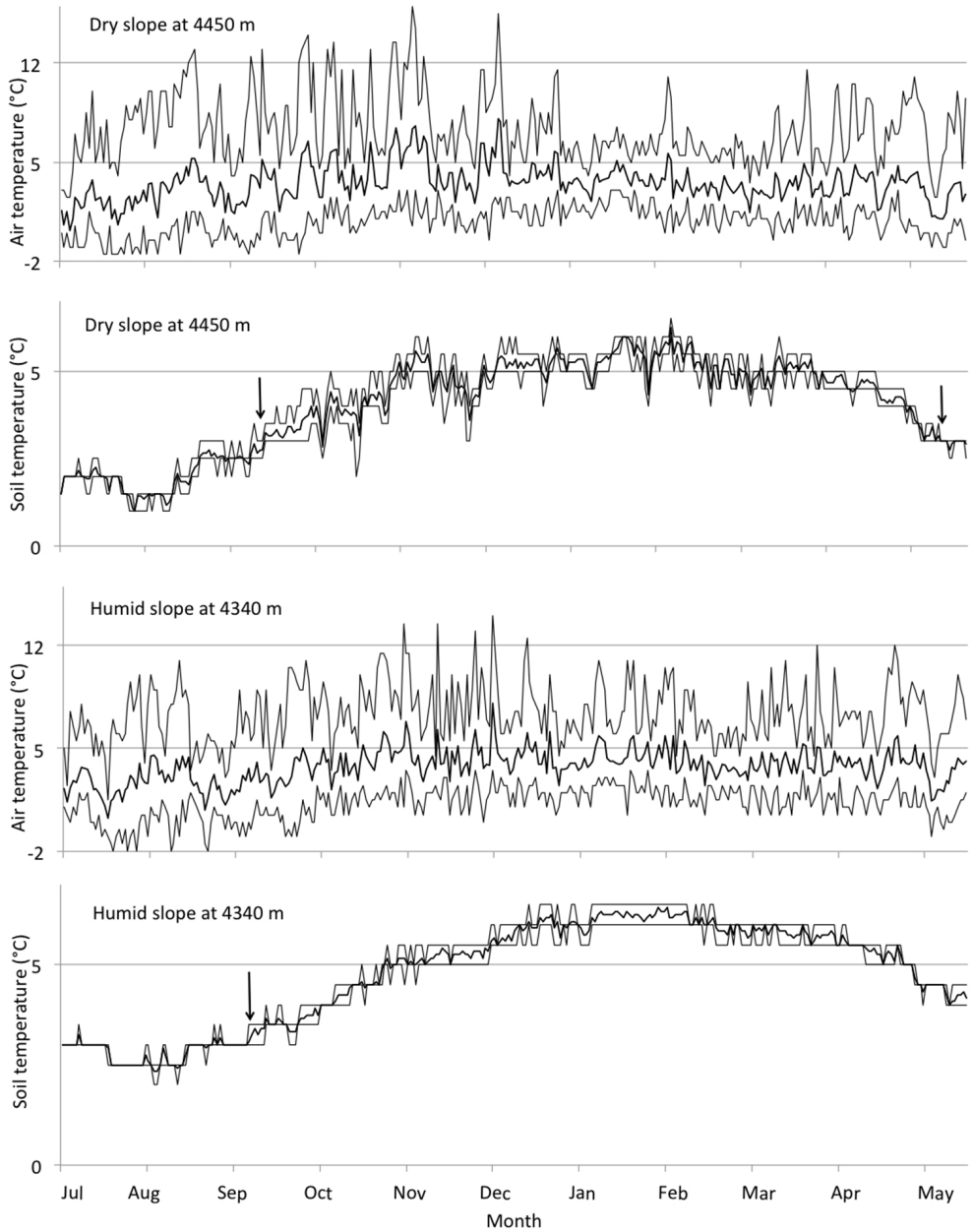

FIGURE 5 | Seasonal variation in air and soil temperatures at the highest sites in dry and humid areas in 2007–2008. Solid lines in the middle indicate daily mean temperatures and dashed lines above and below indicate daily minimum and maximum temperatures. The beginning and the end of the growing season, based on the criteria by Körner and Paulsen (2004), is indicated with arrows. Data from June is missing, and consequently the indication of the end of the growing season at the humid site.

also play a role. First, it is conceivable that local site factors such as microtopography and soil conditions, which are well known to influence tree height (Koch et al., 2004; McNab, 2010; Unger et al., 2012), might have influenced the patterns found by us. However, we do not consider this to be the case since the large number of study plots (46 in total) and the replicates in each elevation belt exclude the impact of single site conditions on our overall findings. Furthermore, we did not find any significant differences in the topographic positions of plots on the different slopes, e.g., with regard to inclination, distance from streams, or distance to rock faces (J. Toivonen et al., unpublished data). The vast majority of plots were located within the same soil class (IMA, Instituto de Manejo de Agua y Medio Ambiente, Gobierno Regional de Cuzco, Peru, 2014). However, it is likely that humid and dry soils have consistent differences due to the climatic influence on soil development (Curtis, 1990). Another possible reason for the differences in tree height might be related to the tree species involved, which differed between the slopes. Testing

Table 2 | Comparison of temperature measurements between the dry and humid slopes in the study region.

Parameter	Dry slope	Humid slope	*t*	*p*
Residuals (mean annual air temperature)	0.13 ± 0.58	−0.33 ± 0.49	1.79	0.09
Residuals (mean annual soil temperature)	0.09 ± 0.65	−0.03 ± 0.50	0.31	0.77
Absolute minimum air temperature	−2.58 ± 1.28	−2.33 ± 0.60	−0.56	0.58
Residuals (absolute minimum soil temperature)	−0.22 ± 0.53	0.09 ± 0.81	−0.73	0.49
Absolute maximum air temperature	23.10 ± 5.65	16.52 ± 0.50	3.87	0.01
Residuals (absolute maximum soil temperature)	0.10 ± 0.73	−0.39 ± 0.58	1.18	0.27
Residuals (mean air temp. of growing season)	0.56 ± 0.45	−0.26 ± 0.37	3.17	0.01
Residuals (mean soil temp. of growing season)	−0.02 ± 0.59	0.18 ± 0.76	−0.48	0.65

For those factors for which significant linear relationships to elevation were recovered when combining data from both dry and humid slopes, t-tests were used to compare the residuals of the dry against the humid sites. For those two parameters without significant elevational trends, the raw values were compared.

this possibility would require reciprocal transplantations between the slopes, which might be problematic because it is likely that the trees would not survive, or have an altered growth, under the "wrong" climatic conditions. While such explanations may have some affect on tree growth, we still consider climate to be the most likely driver of differences in tree height between the slopes. These climate-related differences in tree growth have also been found in many other geographical areas for a wide range of taxa (Kessler et al., 2007; Miehe et al., 2007; Körner, 2012; Paulsen and Körner, 2014).

ARE *POLYLEPIS* FORESTS FOUND UNDER LOWER TEMPERATURE CONDITIONS THAN OTHER TREELINE FORESTS?

The highest stands where microclimatic measurement were carried out on humid slopes (*P. pepei* at 4330 m) had mean soil temperatures for the growing season of about 5.1°C, and the highest stands on dry slopes (*P. subsericans* at 4450 m) of about 4.6°C. These temperatures are close to those reported from *Polylepis* treeline positions elsewhere in the Andes, e.g., mean soil temperatures of the growing season of 4.5–6.0°C at 4000–4100 m in Ecuador (Lauer and Rafiqpoor, 2000, 2002) and of 4.7–5.4°C at 4810 m in western Bolivia (Hoch and Körner, 2005). Other, more short-term measurements show even lower soil temperatures at *Polylepis* treelines in the range of 3–4°C (Kessler and Hohnwald, 1998; Hertel and Wesche, 2008). There is, thus, increasing evidence that high-elevation forests, formed by species of the genus *Polylepis* in the Andes, are found under lower temperature conditions, especially of soil temperatures, than the global mean for high-elevation treeline forests (Körner and Paulsen, 2004; Körner, 2012). There may be various reasons for this. First, as discussed above, it is unclear whether soil temperatures are a truly physiologically limiting factor for tree growth at treeline elevations. Indeed, our study suggests that air temperatures may be physiologically more important due to direct atmospheric coupling of high tree stature. It has been shown that apical meristems of high stature vegetation face lower temperatures than those of short vegetation (e.g., Hadley and Smith, 1987; Wilson et al., 1987; Grace et al., 1989; Körner, 2003). Thus, it is conceivable that *Polylepis* treelines are determined by the same temperature threshold as other treelines, but that this is not reflected by the mean soil temperatures of the growing season. Second, temperature measurements at some other tropical treelines may have been conducted at locations below the potential upper limits of tree growth. For example, the high mean soil temperatures of the growing season of 7.4°C at 3740 m on Mt. Kinabalu, Borneo (Körner, 2012), likely reflect the fact that the rain-swept rocky dome of this mountain lacks soil deep enough for tree growth, resulting in a lowered treeline. Third, species of the genus *Polylepis* may have special functional adaptations to low temperatures that enable them to grow at higher elevations than other tropical treeline species. These adaptations could include decreased leaf size and carbon assimilation rate but higher root tip abundance as found among species of *Polylepis* growing at high elevations compared to species from lower elevations (Toivonen et al., 2013). This reflects the gradual adaptation of the genus from the ancestral habitat in humid cloud forests to increasingly dry and cold conditions (Simpson, 1986; Schmidt-Lebuhn et al., 2006, 2010). Future research directed at identifying the physiological bases of these adaptations, ideally in an evolutionary context, may not only reveal how *Polylepis* has managed to colonize extremely stressful environments, but may also provide insights into the physiological limitations of tree growth at high elevations in general.

CONCLUSION

We studied the role of human impact and climatic conditions on tree height among five species of the high Andean *Polylepis* tree genus. With a mean maximum tree height of 9 m on the humid slopes at 4530 and of 13 m at 4650 m on the dry slopes, we document taller trees than in any previous studies carried out at similar elevations worldwide (Hoch and Körner, 2005; Kessler et al., 2007; Miehe et al., 2007; Bader and Ruijten, 2008). We confirm our hypotheses that tree height is lower in the stands affected by human impact than in the stands in natural conditions, and that tree height is lower on humid than on dry slopes. We also show that humid slopes are colder than dry slopes with respect to air temperatures. Taking into account tree height differences between humid and dry slopes, this suggests that air temperatures are a decisive factor in limiting tree growth at high elevations. Additionally, we show that *Polylepis* treeline

forests grow under lower temperature conditions than the global mean for high-elevation treeline forests (Körner and Paulsen, 2004).

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Chapter 5

The World's highest vascular epiphytes found in the Peruvian Andes

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SHORT COMMUNICATION

The world's highest vascular epiphytes found in the Peruvian Andes

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Abstract The highest elevation epiphytic vascular plant flora ever recorded on a worldwide basis is described from the Cordillera Vilcabamba, southern Peruvian Andes. Three species of fern (*Melpomene*, *Polypodium*: Polypodiaceae) were recorded from *Polylepis pepei* forests at elevations above 4,250 m, with *Melpomene peruviana* reaching almost 4,550 m. A new high-elevation world record for arboreal hemiparasites is also documented, with *Tristerix longebracteatus* (Loranthaceae) being found at c.4,620 m. Climatic conditions of these sites were assessed and are discussed in the light of existing hypotheses on the abiotic conditions limiting epiphytism.

Keywords Arboreal hemiparasites · *Polylepis* · *Melpomene* · Polypodiaceae · Loranthaceae

Introduction

Vascular epiphytes include close to 28,000 species, corresponding to roughly 9 % of the world's vascular plant flora (Zotz 2013a). They are, by definition, higher plants with vascular tissue (xylem and phloem) that grow on other plants, but obtain their nutrients and water entirely from the atmosphere and organic layers on the branches or trunks of their host plants. Epiphyte diversity is highest in humid tropical cloud forests at about 1,000–2,000 m elevation (Cleef et al. 1984; Wolf 1994; Hietz and Hietz-Seifert 1995; Muńoz and Küper 2001; Wolf and Flamenco-S 2003; Bhattarai et al. 2004; Küper et al. 2004; Krömer et al. 2005). This presumably reflects the optimal living conditions for epiphytes, whose growth is limited by light, water and nutrient availability and low temperatures (Benzing 1990). Despite these limitations, vascular epiphytes have also conquered extreme environments ranging from dry semi-deserts (Garcia-Suarez et al. 2003) to cold boreal forests at high latitudes (Maycock 1975; Zotz 2002; Zotz and List 2003).

In mountains, little is known about the upper limits of vascular epiphytic growth. In the northern hemisphere, only two studies in the Himalayas have found epiphytic ferns above 3,500 m (Mehra and Vij 1974) and reaching to 4,000 m (Bhattarai et al. 2004). In the southern hemisphere, high-elevation grammitid fern epiphytes have been recorded from *Polylepis* (Rosaceae) forests in the Andes of South America to 4,000 m in Bolivia (Krömer et al. 2005) and 4,300 m in Ecuador (Lehnert 2013).

Albeit not considered epiphytes, arboreal hemiparasites can also form important components of the canopy in montane forests. All previous records of high-elevation arboreal hemiparasites pertain to the mistletoe family Loranthaceae (2,800 m in the Himalaya, Devkota et al. 2010; 1,250 m in Europe, Dobbertin et al. 2005) with the highest elevational record held by a number of *Tristerix* species from Peru documented at 4,000–4,500 m (Brako and Zarucchi 1993). All members of Loranthaceae form direct contacts with their hosts by means of haustoria, but those which are hemiparasitic also have chlorophyllous leaves which allow them to photosynthesise.

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There is a paucity of information regarding the abiotic conditions that limit epiphytism in temperate zones (Zotz 2003) with it being generally believed that frost occurrence and moisture availability are the key limitations (Zotz 2005). When considering the differences in vascular epiphyte diversity with elevation, temperature (in particular the regular occurrence of frost) has been advocated as the principal limiting factor on vascular epiphytism at higher elevations, but the mechanisms involved are still unknown (Gentry and Dodson 1987; Kessler 2001a, b; Bhattarai et al. 2004; Kreft et al. 2004; Krömer et al. 2005). The elevational limits of arboreal hemiparasitic mistletoes are suggested to be governed, not only by climatic factors, but also by the abundance and availability of avian dispersers (Devkota and Acharya 1996; Ladley and Kelley 1996). Cold and moist habitats found at higher elevations are generally avoided by mistletoe-associated birds leading to a lack of dispersal to these habitats.

At high elevations in the tropics, a further limitation on both epiphyte and arboreal hemiparasite occurrence is the lack of suitable substrate, i.e. the lack of trees at high elevations. The vast majority of high-elevation treeline positions, especially in tropical mountains with their long history of human habitation, have been depressed by at least several hundred metres due to logging, cattle grazing and burning with natural treeline relicts only found as isolated stands in difficult to access areas (Kessler 1995a). This poor accessibility has hindered research on these high-elevation treeline environments.

Polylepis forests are excellent candidates for hosting the world record for high-elevation vascular epiphytes as they are considered to be the world's highest treeline with trees reaching to 4,900 m (Kessler et al. 2014). Our recent exploration in the humid Cordillera Vilcabamba of southern Peru has found *Polylepis pepei* forests reaching much higher elevations than previously documented (Simpson 1979; Kessler 1995b), with forests being found to 4,650 m. These forests host a diverse epiphyte flora including a number of grammitid fern species.

In all previous studies examining vascular epiphytism with relation to elevation, none have reached the absolute elevational limits of epiphytism or studied the abiotic conditions under which these epiphytes can survive. Our study, thus, not only provides a new world record for high-elevation vascular epiphytes, but also insight into the abiotic constraints of epiphytism at their ecophysiological limits.

Material and methods

Sites and study area

The study was conducted in the high mountain areas of the Cordillera Vilcabamba, Province of La Convención, Cusco region, in the southern Peruvian Andes (S13° 10′, W73° 03′, >4,250 m). The climate of the area is relatively humid from receiving updrafts of humid air from the Amazon basin, and there is a clear wet season from November to April. Diurnal temperature fluctuations are very pronounced, especially in the dry season. The vegetation of the study region contains floristic elements of both the humid páramo, found in northern Peru (Marcelo-Peña et al. 2006; Tovar et al. 2012), and the dry puna, which occupies the majority of the high-elevation landscapes of central and southern Peru (Wilcox et al. 1986, 1987; Florez-Martínez 2005).

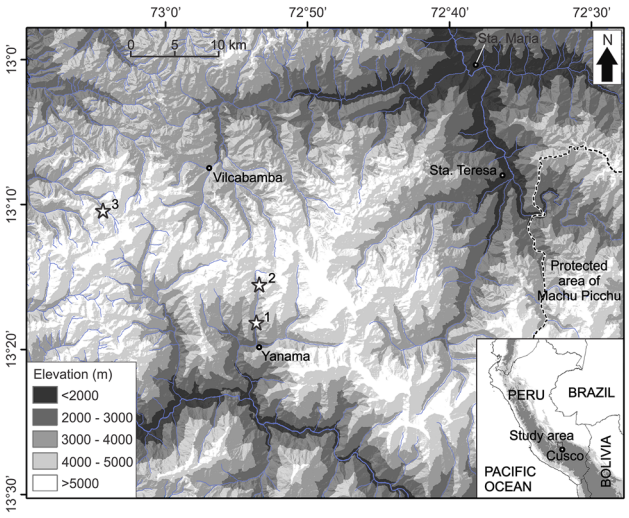

Fig. 1 Map of the study area showing the three study sites (denoted by *numbered stars*). ASTER DEM raster map provided by METI and NASA Land Processes Distributed Active Archive Center

Three sites, which were comprised of *Polylepis pepei* forests found at their upper elevational limits, were studied within the Cordillera Vilcabamba (Fig. 1 and ESM). Site 1 was located within the highest forest found on the north side of the lower Phacchaq valley, 4 km north of Yanama, district of Santa Teresa (S13° 17′ 02.0″ W72° 50′ 02.6″, 4,200–4,650 m). Site 2 was located within the forested mountain ledges on the uppermost eastern portion of the Phacchaq valley, 8.5 km north of Yanama, district of Santa Teresa (S13° 15′ 16.9″ W72° 50′ 22.5″, 4,250–4,490 m). Site 3 was located on the forested large prominent ledge on the south facing cliff at the end of the Totora-Purkay valley, 4 km east of the Totora-Purkay village, district of Vilcabamba (S13° 11′ 00.2″ W73° 03′ 07.6″, 4,400–4,550 m).

Data collection

Voucher specimens of the epiphytes encountered were collected and identified in the herbarium and are deposited at the herbaria CUZ, LPB, STU and Z. Plant nomenclature follows W3TROPICOS (Solomon 1999). Elevation was measured using a Garmin Etrex H handheld GPS device

which was tested at landmarks with documented elevations and found to have a precision of ±10 m.

Relative air humidity and temperature were recorded using digital dataloggers (DS1923 Hygrochron iButtons; Hubbart et al. 2005). Dataloggers were placed at sites 1 and 2 (Fig. 1, ESM), on a field trip in May 2012. The datalogger at site 1 was placed at c. 4,566 m (S13° 17′ 01.4″ W72° 50′ 01.5″), whilst the datalogger at site 2 was placed at c. 4,494 m (S13° 15′ 13.8″ W72° 50′ 24.0″). The elevational difference of c.72 m between sites was deemed to have little or no effect in explaining the differences in climate exhibited at each site. The dataloggers were placed on raised platforms 20 cm from the ground surface. These platforms were shielded from direct sunlight and rain and were located close to where the epiphytes were encountered. Dataloggers were placed at either c.40 or c.20 m distance and either c.40 or c.3 m higher elevation than the highest epiphyte specimens encountered at sites 1 and 2, respectively. These differences in elevation and distance of the dataloggers from the highest epiphytes encountered were not deemed significant and so the climatic variables recorded can be generally inferred as those experienced by epiphytes at these sites. The dataloggers were set to record at intervals of 2 h for a period of 12 months and were recollected on a fieldtrip in May 2013. Length of the growing season was calculated as the number of days per year where temperature rose above 5 °C during the day (see Körner 2011 for other definitions). This definition was used as higher plants are understood to need temperatures above 5 °C to grow, mature their seasonal foliage and reproduce (Körner 2003).

Results

High-elevation vascular epiphytes

Three fern species were found growing epiphytically on *Polylepis pepei* trees at elevations above 4,250 m (Table 1) in all three sites. Two species of *Melpomene*, *M. peruviana* and *M. personata*, were found to elevations above 4,500 m with *M. peruviana* occupying the highest elevation record at c.4,542 m. *Melpomene peruviana* was the more common species to be found at high elevations, being present at all three sites at elevations above 4,500 m. *Melpomene personata* was less frequent at these elevations with only one specimen being found above 4,500 m at site 3, but being found at a lower elevation of c.4,250 m at site 1. Both *Melpomene* species were only found as epiphytes in the study area, although higher elevation records have been found from terrestrial dwelling specimens of the same species (Solomon 1999; Lehnert 2013), meaning these species are 'facultative epiphytes' according to Zotz (2013a, b). *Polypodium chrysolepis* occupied the lowest elevations being found to c.4,288 m and was found both epiphytic and terrestrial in the study area and so can also be classed as a 'facultative epiphyte'. All vascular epiphyte species were found to occupy the tree bole or primary branches and were found at heights of 1–2 m from the forest floor. A hemiparasitic member of the family Loranthaceae, *Tristerix longebracteatus*, not considered to be a true epiphyte, occupied the highest elevations being recorded growing on both *P. pepei* and *Gynoxys cuzcoensis* Cuatrec. (Asteraceae) trees up to 4,618 m. This species generally occupied the outer canopy and was found at heights of 3–8 m from the forest floor.

Table 1 List of epiphytic vascular plants and arboreal hemiparasites recorded at elevations above 4,250 m with the highest elevation recorded for each species and details of the specimen voucher

Species	Highest elevation recorded (m)	Voucher
Vascular epiphytes		
Melpomene peruviana (Desv.) A.R. Sm. & R.C. Moran	4,542	*Sylvester 1869*
Melpomene personata Lehnert	4,527	*Sylvester 1867*
Polypodium chrysolepis Hook.	4,288	*Sylvester 1585*
Arboreal hemiparasite		
Tristerix longebracteatus (Desr.) Barlow & Wiens	4,618	*Sylvester 2024*

The elevational position of the treeline was found to be c.4,650 m at all of the sites, but this elevation was only reached, and the highest trees checked for epiphytes, at site 1. The elevation reached at sites 2 and 3 was 4,550 and 4,570 m, respectively, due to difficulties of access to the highest forests.

Site microclimate

There was a distinct dry season from May to November which also coincided with the coldest months of the year (Fig. 2a). Diurnal temperature fluctuations were very pronounced with the coldest days having an average difference of 14.6 °C between the highest and lowest values and the greatest temperature difference of 17.6 °C in the month of August. Site 2 had generally lower temperatures than site 1 (Table 2; Fig. 2a) with a lowest temperature of −5.5 °C reached in the months of August and September. The number of days on which temperatures dropped below 0 °C was also greater for site 2 with 131 days through the months of April–October. In comparison, site 1 only experienced 23 days during the months of June–September where temperatures dropped below 0 °C. The longest frost-free period (i.e. the greatest number of days where temperatures did not

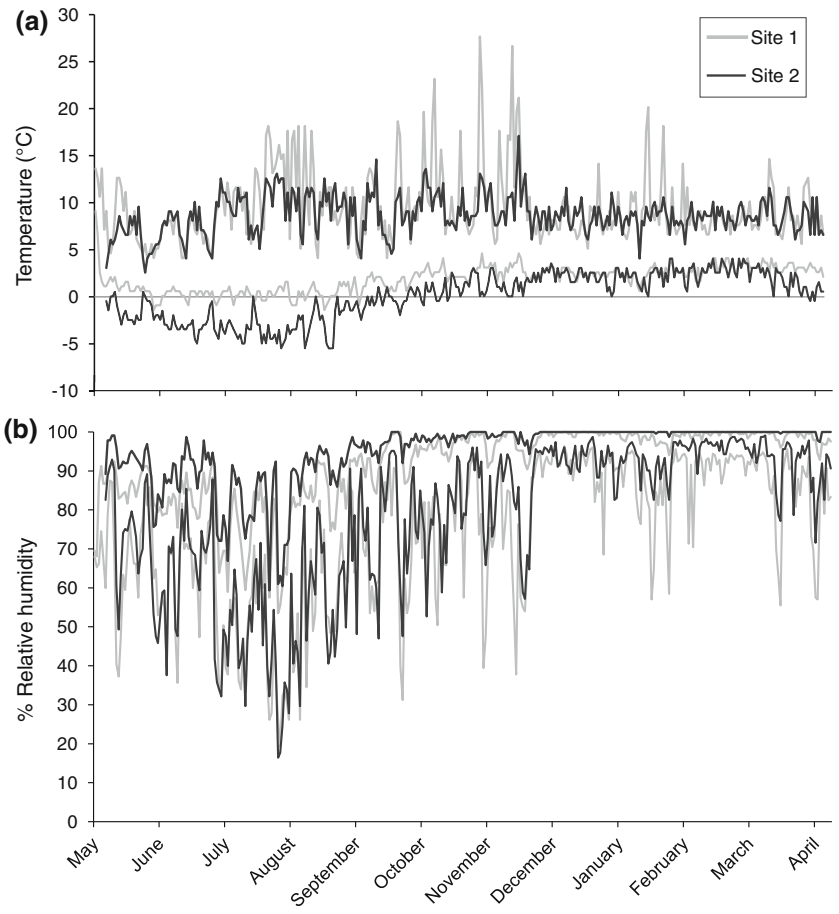

Fig. 2 Minimum (*thin lines*) and maximum (*bold lines*) air temperature (**a**) and relative air humidity (**b**) at sites 1 (*grey*) and 2 (*black*) over the period of 1 year

Table 2 Air temperature and relative humidity records from sites 1 and 2

	Site 1	Site 2
Absolute minimum temperature (°C)	−1.4	−5.5
Absolute maximum temperature (°C)	27.7	17.1
Mean daily minimum temperature (°C)	1.9	0.1
Mean daily maximum temperature (°C)	9.5	8.7
Mean daily temperature (°C)	4.2	3.3
Days/year where temperature dropped below 0 °C	23	131
Length of frost-free period (days)	270	168
Growing season (no. of days where temperature rises above 5 °C)	351	352
Absolute minimum relative humidity (%)	14.2	13.4
Mean daily relative humidity (%)	80.9	86.3
Days/year where relative humidity passed 90 %	184	247
Days/year with fog occurrence (relative humidity passed 99 %)	125	178

drop below 0 °C) was documented from site 1 with 270 days from 14th September 2012 till 11th June 2013. Site 2 had a shorter frost-free period spanning 168 days from 25th October 2012 to 11th April 2013. The length of the growing season, calculated as the number of days where temperature rose above 5 °C, was similar for both sites and was almost year round with 351 days for site 1 and 352 days for site 2. Site 2 had a generally higher relative humidity compared to that of site 1 (Table 2; Fig. 2b) with 247 days where relative humidity reached past 90 % as opposed to 184 for site 1. The daily occurrence of fog, whereby air relative humidity reaches past 99 % on any given day in the year, was also higher in site 2 with 178 days as opposed to 125 days in site 1.

Discussion

Our study documents, to our knowledge, the highest vascular epiphytes and highest arboreal hemiparasites found to date. In the following, we place these records in relation to potential limitations to epiphyte growth at high elevations.

Abiotic constraints on the elevational limits of vascular epiphytes

As our dataloggers were originally intended to measure climatic conditions for the ground vegetation within the

studied forests, we did not situate them exactly where vascular epiphytes were encountered (i.e. on the tree bole and primary branches, 1–2 m from the forest floor), but rather at the tree base. Furthermore, they were placed at slightly higher elevations than the highest epiphyte specimens encountered. Our microclimatic data may, thus, not reflect actual conditions at the highest localities where vascular epiphytes were found. Other studies have found higher sections of trees to experience more pronounced fluctuations in temperature and humidity and be generally drier compared with tree bases (Parker 1995; Karger et al. 2012). Therefore, it is likely that the conditions experienced by the species in our study region are more extreme than those that are presented here. Despite these limitations, our data provide approximate measurements of the climatic conditions at the growth sites of the epiphytes and are probably the most reliable data obtained to date at the upper limit of tropical vascular epiphytism.

Previous studies have placed temperature and, in particular, the occurrence of frost as the principal limiting factors on the elevational distribution of vascular epiphytes (Krömer et al. 2005 and references therein). The *Melpomene* species demonstrate a great physiological tolerance to low temperatures, experiencing up to 131 days of freezing temperatures per year. However, if we consider the growing season for ferns at these elevations as being days per year in which temperatures rise above 5 °C (Körner 2003), then each fern has almost a year-round growing season. These temperatures are similar to those experienced in *Polylepis pepei* forests at 4,000 m in the Bolivian Andes (Kessler and Hohnwald 1998; Krömer et al. 2005) and do actually appear fairly amenable for fern epiphyte survival if compared with other studies outside of the Andes. Bhattarai et al. (2004) found the growing season for epiphytic ferns in the Himalayas to be significantly shorter with c.120 days/year in comparison with >351 days/year in the Cordillera Vilcabamba sites. This difference reflects the stronger climatic seasonality of the Himalayas (c. 28°N) as compared to our study area (13°S).

If we compare this temperature data with ecological data on temperate vascular epiphytes from higher latitudes, specifically *Polypodium vulgare* at 1,300 m in the Swiss Alps (c. 47°N; Zotz 2002), it can be seen that the temperatures that *Melpomene* experience at these elevations are not that low compared with what *P. vulgare* has to endure. The mean yearly absolute minimum temperature, taken from 36 years of temperature recording, was −16.4 °C, much lower than the −5.5 °C absolute minimum experienced in the study area. The physiological tolerance of *P. vulgare* to cold temperatures may be much greater than the *Melpomene* species studied here, although there are other variables that should be compared (i.e. number of frost days, length of growing season, annual mean minimum temperature) to assess the cold limits of vascular epiphyte life.

We present the first data on air relative humidity recorded from sites where temperate vascular epiphyte growth has been documented. Both sites 1 and 2 experienced a high relative humidity with over half the year having days where relative humidity rose above 90 %. Interestingly, no vascular epiphytes have been noted from *Polylepis* forests above 3,800 m in the neighbouring Cordillera Vilcanota, which experience similar temperature regimes to the current sites studied (Sylvester et al. *unpubl. data*). Therefore, it could be conjectured that the comparatively drier climates of these areas (Toivonen et al. 2011) likely inhibit the establishment and survival of vascular epiphytes that are wholly dependent on precipitation and atmospheric humidity for their water supply.

Biotic constraints on the elevational limits of vascular epiphytes

It comes as little surprise that the grammitid fern genus *Melpomene* holds the world record for the highest elevation vascular epiphyte. Previous studies have already found this genus to occupy very high elevations in the Andes (Krömer et al. 2005; Lehnert 2013). What special physiological characteristics pertain to the *Melpomene* species that allow them to grow at these elevations remains a question that awaits experimental analysis.

Habitat availability appears to be one of the main constraints on the elevational limit for growth of the two *Melpomene* species in the Cordillera Vilcabamba. The species definitely did not seem at their ecophysiological limits and were common in all the high-elevation forests studied with all populations found to be reproducing (although the viability of the spores would need to be tested to verify this claim). This implies that these high-elevation populations are source populations and not sink populations, as suggested by Bhattarai et al. (2004) who found ferns in the alpine environment to be mainly sink populations of subalpine species which can barely tolerate the harsh and stressful open alpine habitat. At both sites 2 and 3, where *Melpomene* species were found epiphytic in the highest trees encountered, the forests extended to even higher elevations than those that were possible to reach in the present study. Therefore, it is plausible that the upper elevational limits on vascular epiphyte growth may be even higher than presently documented.

High-elevation arboreal hemiparasites

This study also gives a new elevational world record for arboreal hemiparasites with *Tristerix longebracteatus* being found at c. 4,620 m. The species was a common constituent of the *Polylepis pepei* forests at site 1, but its absence in sites 2 and 3 could relate to either ecophysiological limitations or

habitat preferentiality of their avian dispersers. Site 1 had a more amenable climate compared to site 2 with fewer days of frost occurrence and air temperatures generally warmer that is likely to be more favourable habitat for arboreal hemiparasites and their associated avian dispersers. However, with no data collected on avifaunal composition and fruit dispersal specifities from the sites, we cannot disentangle the importance of ecophysiological limitations and avian dispersers in shaping the elevational limits of arboreal hemiparasites.

Conclusion

This is the first study to document vascular epiphytes, arboreal hemiparasites and their abiotic conditions from elevations over 4,000 m. A number of factors lend themselves to the Cordillera Vilcabamba holding the world record for high-elevation vascular epiphytes and arboreal hemiparasites; a combination of (a) humid climate, caused by updrafts of moisture laden air from the Amazon, and (b) presence of high-elevation forests, create the ideal niche for survival at elevations previously undocumented. Temperature, substrate and water availability are all conjectured as being important in determining the upper hard boundary of vascular epiphyte survival, whilst the elevational limits of arboreal hemiparasites could also be linked to the availability of avian dispersers. Further research is required to resolve which of these factors takes precedence in determining these elevational limits.

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Electronic Supplementary Material S1 to Sylvester SP, Sylvester MDPV, Kessler M (2014) The world's highest vascular epiphytes found in the Peruvian Andes. Alpine Botany

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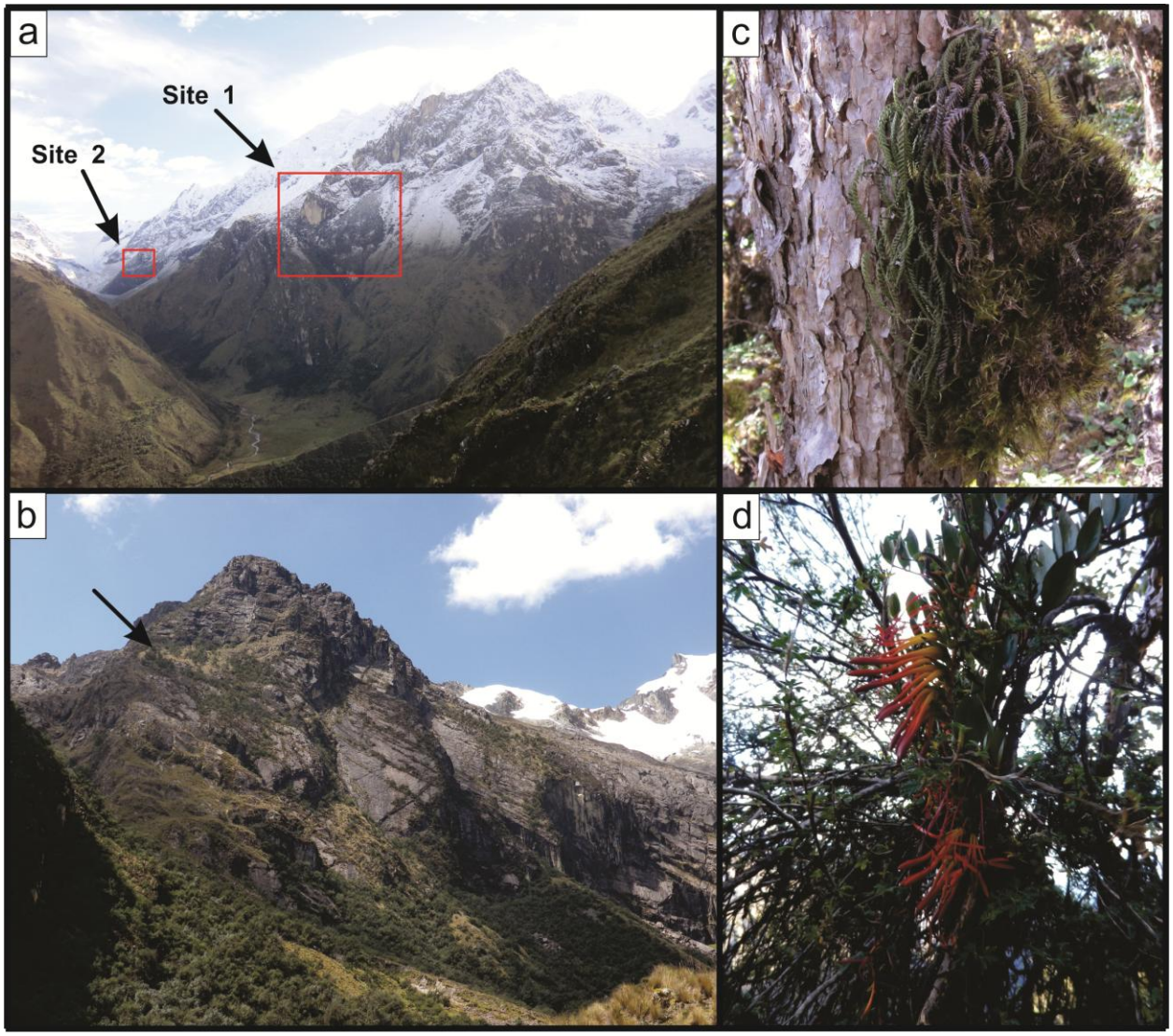
Photographs showing a) the positions of sites 1 and 2; b) site 3, with the arrow indicating the location of the highest vascular epiphyte encountered; c) *Melpomene peruviana,* the highest elevation vascular epiphyte, collection *S.P. Sylvester 2025*. The photo also shows a good example of the characteristically flaky *Polylepis* bark; d) *Tristerix longebracteatus*, the world's highest arboreal hemiparasite found parasitizing *Polylepis pepei* trees at 4618 m, collection *S.P. Sylvester 2024*.



Chapter 6

An updated checklist and key to the open-panicled *Poa*'s (Poaceae) of Peru including 3 new species, *Poa ramoniana*, *Poa tayacajaensis* and *Poa urubambensis*

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An updated checklist and key to the open-panicled *Poa*'s (Poaceae) of Peru including 3 new species, *Poa ramoniana*, *Poa tayacajaensis* and *Poa urubambensis*

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Abstract

A revised and updated checklist and key to *Poa* species with open panicles from Peru is provided which includes previously circumscribed *Dissanthelium* species and new taxon records and undescribed species discovered since the most recent taxonomic treatments. *Poa compressa*, *Poa grisebachii* and *Poa leioclada* are recorded from Peru for the first time. A number of species epiphets are placed in synonymy: *Poa carazensis*, *Poa ferreyrae* and *Poa tovarii* are synonimised under the name *Poa fibrifera*; *Poa adusta* and *Poa pilgeri* are synonimised under *Poa candamoana*; *Poa superata* is synonimised under *Poa grisebachii*; *Poa paramoensis* is synonimised under *Poa huancavelicae*. Included within this treatment are three new species, *Poa ramoniana*, *Poa tayacajaensis* and *Poa urubambensis,* which are described and illustrated from southern Peru. *Poa ramoniana*, found growing by lakes in high elevation puna grassland, appears like a small form of *Poa glaberrima*, but differs by being extensively rhizomatous and growing to only 5 cm tall. *Poa tayacajaensis*, found from shrublands on Andean slopes, bears similarities to *Poa aequitoriensis* but differs by having shorter lemmas which are pubescent between the veins, densely scabrous sheaths with smooth, glabrous throats, and shorter ligules. *Poa urubambensis* is distinct from all other members of *Poa* with open-panicled inflorescences by the combination of spikelets with glabrous lemmas and callus, and notably small anthers. *P. urubambensis* is a common element of undisturbed puna vegetation in the Cordillera Urubamba, southern Peru, being associated with *Polylepis* forest understory.

Introduction

The genus *Poa* Linnaeus (1753: 67) is considered the largest genus of the Poaceae, containing over 500 species with a large distribution across temperate areas of the globe (Soreng et al. 2003 onwards). The first taxonomic treatment of *Poa* from Peru comes from Hitchcock's (1927) 'The grasses of Ecuador, Peru and Bolivia' in which he mentions 17 species of *Poa* present in Peru. Standley (1936) then developed on this work for the Flora of Peru series and produced the first treatment of purely Peruvian grasses in which he added *P. aequatoriensis* to the country record, bringing the total number of Peruvian *Poa* to 18. Following this, the renowned Peruvian agrostologist, Óscar Tovar Serpa, began his life-long work on Peruvian grasses producing a number of publications related to *Poa* (Tovar 1965, 1974, 1984, 1986) until his

largest cumulatory work in 1993 where he provided a concise treatment of all grasses from Peru (Tovar 1993).

Tovar's (1993) most up-to-date taxonomic treatment, and the Checklist for Peru (Brako & Zarucchi 1993), that was published in the same year, considered the country to have either 40 or 41 species of *Poa*, respectively. This number has since varied due to taxonomic revision placing certain names in synonymy (Soreng et al. 2003 onwards) and discoveries of undescribed species (Negritto & Anton 2006; Soreng & Peterson 2010). Recent phylogenetic studies (Gillespie et al. 2008; Refulio-Rodríguez et al. 2012) have also found the genus *Dissanthelium* Trinius (1836: 305) to be nested within *Poa* subg. *Poa* supersect. *Homalopoa* (Dumort.) Soreng & L.Gillespie (Gillespie et al. 2007: 432) and, given the, sometimes, unclear morphological delimitation between *Poa* and *Dissanthelium*, it seems prudent that taxonomic treatments of *Poa* should include those species previously assigned to *Dissanthelium*.

Following the discovery of three more undescribed species, the aim of this study has been to gain an up-to-date picture of the species of *Poa* present in Peru with open-panicled inflorescences. Previous estimates of the number of open-panicled *Poa* species of Peru were 21 and 20 according to Tovar (1993) and Brako & Zarucchi (1993), respectively. Panicle characteristics are an 'artificially' good way of separating out Peruvian *Poa* into two distinct groups. All taxonomic treatments of *Poa* in Peru (Hitchcock 1927; Standley 1936; Tovar 1993), Bolivia (Renvoize 1998) and Ecuador (Hjorth 1991) have provided diagnostic keys that, in the first couplet, separate species into those with a congested spike-like panicle, with panicle branches appressed, and those with an open-panicled inflorescence, the branches spreading. We believe this to be a convenient and reliable character in separating out the Peruvian *Poa*'s and provide an updated checklist and key to all described *Poa*'s of Peru with an open-panicled inflorescence.

The new species, *Poa urubambensis*, was found during recent botanical exploration in remote areas of the Cordillera Urubamba, southern Peru, for a large scale ecological study attempting to reconstruct the potential natural vegetation and soils of the high-elevation puna grasslands of southern Peru (see Heitkamp et al. 2014 and Sylvester et al. 2014 for pilot studies). In this study, pristine zonal vegetation, only accessible with mountaineering equipment, was compared with surrounding slopes which have been grazed and burnt consistently over millennia (Thompson et al. 1988; Chepstow-Lusty et al. 1996, 2009; Kuentz et al. 2011). *Poa urubambensis* was a common element in undisturbed puna grassland vegetation, being found associated with *Polylepis* Ruiz & Pav. (1794: 80) forests from three different sites. This species is morphologically distinct from all other species of Peruvian *Poa* by a combination of an open-panicled inflorescence, glabrous lemma and callus, and unusually small anthers.

Whilst checking Peruvian specimens of *Poa* with open-panicled inflorescences, a further two undescribed species, *Poa ramoniana* and *Poa tayacajaensis*, were discovered. *Poa ramoniana* was discovered from collections by eminent Peruvian botanist, Ramón Alejandro Ferreyra, from the Junín province. This species can be distinguished by completely glabrous and smooth spikelets, small stature (<5 cm tall) and extensively rhizomatous habit. *Poa tayacajaensis* was discovered from collections by the renowned Peruvian agrostologist, Óscar Tovar Serpa, from the province of Tayacaja, Huancavelica. This species bears similarities to *Poa aequitoriensis* but differs by having lemmas which are generally shorter (2.8–3.7 mm long),

pubescent between the veins, and by more densely scabrous sheaths, with more or less smooth glabrous throats, ligules generally shorter.

During revision of Peruvian specimens, new species records have also come to light with *Poa* cf. *leioclada,* previously considered endemic to Ecuador, and *Poa grisebachii,* previously considered endemic to Argentina (Giussani et al. 2012), being reported for the first time from Peru. *Poa compressa* L., originating from Europe, is also reported for the first time. Revision has also led to certain names being placed in synonymy. The three species, *Poa carazensis*, *P. ferreyrae,* and *P. tovarii,* have been found to be morphologically indistinct from *Poa fibrifera* and have been placed under that name. *Poa adusta,* only known from the type collection with large uncertainty surrounding its origin and identity, and the recently described *Poa pilgeri* Negritto & Anton (2006:87) are synonimised under *Poa candamoana*. Specimens of *Poa superata,* previously known only from Argentina, have been collected from Peru and have been found to be morphologically indistinct from *Poa grisebachii*, also previously considered endemic to Argentina, and have, thus, been placed in synonymy under that name. *Poa paramoensis,* previously considered endemic to Ecuador (Laegaard 1998), has been found to be morphologically indistinct from *Poa huancavelicae* and so has been placed as a synonym of that taxon. Reports of *Poa bromoides*, *Poa lilloi* and *Poa supina* for Peru have also been found to be erroneous and, as such, these species have been removed from the country record.

Due to these new discoveries and changes in nomenclature we now recognize 27 species of *Poa* from Peru with open-panicled inflorescences. We provide locality information using verified specimens and discuss nomenclatural and taxonomic attributes of each species. Included within this, we describe three new species, *Poa ramoniana*, *Poa tayacajaensis* and *Poa urubambensis*, based on morphological studies of dry and living material in collections and field studies. Two key's are also provided to aid with identification of the open-panicled *Poa* from Peru. The key provided in the main document uses anther length to separate taxa at the beginning of the key whilst the supplementary key (Appendix 1) uses lemma indumentum. It is hoped that, through the combination of these two keys, users will have a better chance of accurately identifying *Poa* specimens from Peru.

Taxonomy

Materials and methods

In this treatment, glabrous refers to without pubescence. Smooth indicates no prickle-hairs with broad bases and/or hooked or pointed apices (i.e. pubescence can occur on a smooth surface, and a scabrous surface can be glabrous). Specimen localities in the checklist are cited by region (also called 'departamento') (capital letters) and then province. Only herbaria where specimens have been checked and verified by the authors have been cited. Almost all *P.M. Peterson* collections are duplicated at USM, although the USM duplicates have not been checked. Excluded species are presented at the end of the checklist.

Key to the open-panicled species of *Poa* in Peru

1. Glumes exceeding the distal florets; spikelets 2-flowered; lemmas 3 (rarely 5)-veined, glabrous, smooth or scaberulous; low tufted (sometimes rhizomatous in *P.trollii*) perennial plants mostly less than 10 cm tall; panicles 1–3.3 cm long 2
– Glumes shorter than the proximal floret; spikelets 2–4(–6)-flowered; lemmas 5(or 7)-veined, glabrous or pubescent, smooth or variously scabrous; annual or perennial plants of various habits, ranging mostly from 10–120 cm tall; panicles longer (sometimes short in the annuals) 4

2 (1). Anthers 2–2.2 mm long; lemmas smooth throughout; plants sometimes rhizomatous ..... *P. trollii*
– Anthers <1 mm long; lemmas scaberulous, at least on the keels (rarely smooth in *P.calycina*); plants densely tufted 3

3 (2). Leaf blade abaxial surface shiny with leaf veins indistinct..... *P.calycina*
– Leaf blade abaxial surface dull with leaf veins apparent ..... *P.swallenii*

4 (1). Longest anthers of proximal florets 0.2–1.5 mm long 5
– Longest anthers of proximal florets (1.2–)1.6–3.2 mm long 14

5 (4). Plants annual; palea keels distinctly pubescent in part (very rarely glabrous) always without any hooks; web absent 6
– Plants perennial; palea keels glabrous or pubescent in part, but always scabrous in part; web absent or present 7

6 (5). Anthers 0.2–0.5(–0.6) mm long; panicle branches ascending, spikelets usually crowded; foliage light green; plants ephemeral ..... *P.infirma*
– Anthers 0.6–1 mm long; panicle branches ascending to spreading, spikelets loosely arranged; foliage usually darker green; plants infrequently persisting for more than one season…*P.annua*

7 (5). Culm nodes strongly compressed, lower culm nodes exposed; culms wiry; strongly rhizomatous with isolated shoots ..... *P.compressa*
– Combination of characters not as above; culm nodes terete or slightly compressed, lower culm nodes usually held within sheaths; culms varying from wiry to robust; tufted or rhizomatous 8

8 (7). Callus glabrous ..... *P.urubambensis*
– Callus webbed, i.e. with long silky hairs (sometimes sparse) emerging from below the lemma keel (at least of the lower florets) 9

9 (8). Leaf blades filiform or slightly broader, involute or subinvolute towards the base, 0.5–2 mm wide when expanded; lower lemma 3–4 (5?) mm long, glabrous; web only (web sometimes v. short and sparse, and present on basal florets only)……*P.pauciflora*

– Leaf blades flat or folded, usually >2 mm wide when expanded; lower lemma 2.3–6 mm long, variously glabrous or pubescent..... 10

10 (9). Upper ligules 0.9–2(–3) mm long, truncate; plants distinctly rhizomatous; lower sheaths smooth, sometimes lightly pubescent; lower lemma keel and marginal veins distinctly pubescent; spikelets with 2–6 florets; all florets of spikelets hermaphroditic (sometimes anthers aborted late in development) ..... *P.pratensis*
– Combination of characters not as above; upper ligules 0.2–10 mm long, acute or rarely truncate; plants tufted (weakly rhizomatous in *P.huancavelicae*); lower sheaths smooth to densely scabrous; spikelets with 2–3 florets; upper floret within spikelets sometimes pistillate, with rudimentary stamens 11

11 (10). Leaf blades folded, apex prominently naviculate (prow-tipped); plants weakly rhizomatous; lemma keels and marginal veins smooth or asperulous, glabrous; web only…… ..... *P.huancavelicae*
– Leaf blades flat, apex not, or not prominently, naviculate; plants tufted, occasionally stooling and rooting at nodes; lemma keels short pubescent in the lower ½, sometimes sparingly so on the marginal veins near the base(rarely glabrous in *P.aequatoriensis*) 12

12 (11). Spikelet proximal lemmas pubescent on keel, lateral, and marginal veins; distal lemmas pubescent between the veins; sheaths densely scabrous; ligule 2–3.5 mm long ..... *P.tayacajaensis*
– Combination of characters not as above; spikelet proximal lemmas glabrous or sparingly pubescent on the keel, and sometimes marginal veins; distal lemmas often glabrous throughout; sheaths smooth to densely scabrous; ligule 1–10 mm long 13

13 (12). Lower culm sheaths usually puberulent in the throat margins and/or along the collar margins, surfaces smooth to lightly scabrous; upper culm leaf ligules 1–5(–7) mm long, abaxially puberulous or scabrous; lowest floret of spikelets hermaphroditic, upper florets commonly pistillate; spikelets 3.5–5 mm long; lower lemma 3.6–4 mm long, intermediate veins faint to moderately pronounced; palea keels usually finely scabrous to some degree; anthers mostly 0.6–1.5 mm long…… *P.aequatoriensis*
– Lower culm sheaths glabrous in the throat margins, surfaces nearly smooth to densely scabrous; upper culm leaf ligules 4–10 mm long, abaxially smooth or faintly scabrous; all florets of spikelets hermaphroditic; spikelets 2.3–3.5(–4) mm long; lower lemma 2.3–3(–3.5) mm long, intermediate veins distinctly pronounced; palea keels usually muriculate, sometimes minutely scabrous; anthers 1.3–2.1 mm long. ..... *P.trivialis*

14 (4). Lemmas glabrous, smooth or scabrous (rarely sericeous at the base in *P.ramifera*); callus glabrous 15
– Lemmas, at least of the upper florets, pubescent or villous in their lower half (rarely scabrous-pubescent in *P.kurtzii*), or glabrous but then callus webbed, i.e. with long silky hairs emerging from below the lemma keel; callus glabrous or webbed 23

15 (14). Culms erect, aerially branching well up the culm with lateral shoots that persist and flower in subsequent seasons……..*P.ramifera*
– Culms not branching, or branching only near the base, or from decumbent culms 16

16 (15). Lemmas surface usually completely smooth 17
– Lemmas slightly to strikingly scabrous between and on veins 20

17 (16). Plants 4–6 cm tall; rhizomatous; ligule <1 mm long ..... *P.ramoniana*
– Plants > 10 cm tall; tufted or, if rhizomatous > 100 cm tall; ligules 2–7 mm long. 18

18 (17). Leaf blades smooth throughout, (2–)4–9 cm long, 1–2(–2.5) mm wide when blade flattened ..... *P.glaberrima*
–Leaf blades densely scabrous throughout, 8–40 cm long, 3–10 mm wide when blade flattened 19

19 (18). Leaf blades conspicuously conduplicate; plants 25–35 cm tall, tufted .. *P.gilgiana*
– Leaf blades flat; plants 100–150 cm tall, rhizomatous ..... *P.ayacuchensis*

20 (16). Leaf blades involute (rarely conduplicate in *P.kurtzii*), densely scabrous (at least abaxially), firm to rigid; plants tufted; ligule (2.5–)5–15 mm long 21
– Leaf blades flat or folded, rarely involute, glabrous or lightly scabrous, lax or firm; plants erect (*P. fibrifera*) or rhizomatous (*P. oscariana*), sometimes tufted; ligule 1–7(–9) mm long. 22

21 (20). Ligule 8–15 mm long; panicles narrowly ovate, panicle branches ascending and subappressed, panicles included in the sheaths; lemmas scabrous ..... *P.pearsonii*
– Ligule (2.5–)5–8 mm long; panicles amply ovate, panicle branches patent or reflexed, panicles exerted; lemmas scabrous-pilose ..... *P.kurtzii*

22 (20). Lower leaf sheaths often fibrous; ligules 1.5–5(–6) mm long; blades lax; spikelets 3–5 flowered, 5–9 mm long; anthers 2.4–3.5 mm long; rachilla internodes well exposed…*P.fibrifera*
– Lower leaf sheaths not fibrous; ligules 6–9 mm long; blades somewhat firm; spikelets 2–3 flowered, 4.5–5 mm long; anthers 1.8–2 mm long; rachilla interrnodes short (compare with *P. gilgiana*) ..... *P.oscariana*

23 (14). Callus glabrous; lemmas (at least the distal ones within a spikelet) softly villous-pubescent in their lower half 24
– Callus webbed, i.e. with long silky hairs (sometimes sparse) emerging from below the lemma keel (at least of the lower florets); lemmas glabrous or distinctly to sparsely villous or serious pubescent along the keel and marginal veins only 27

24 (23). Plants (30–)60–150 cm tall; Leaf blades flat, , sometimes folded towards their apices, usually more than 3 and up to 10 mm wide; inflorescence branches commonly verticillate; plants (sub-)rhizomatous with extravaginal shoots (if blades rather firm and folded but broad as in *P. horridula*, compare with *P. gilgiana*, possibly hybrids) ..... *P.horridula*
– Plants usually <35 cm tall; leaf blades involute to narrowly convolute and 0.5–2 mm wide, or flat to folded and 1–5 mm wide in *P.grisebachii*; inflorescence branches solitary or paired (often 3 branches in basal nodes of *P.grisebachii);* plants usually with only intravaginal shoots, (rarely sub-rhizomatous in *P.grisebachii)* 25

25 (24). Leaf blade abaxial surface densely scabrous; ligule (2.5–)5–8 mm long, acute; lemmas scabrous-pilose; plants of semi-arid habitats ..... *P.kurtzii*
–Leaf blade abaxial surface glabrous to scaberulous with prickles or hooks usually restricted to the leaf margin; ligule 0.5–3 mm long, truncate; lemmas pilose-villose towards base; plants of mesic or more arid habitats 26

26 (25). Leaf blades usually involute (no extravaginal shoots), apex narrowly but abruptly naviculate; spikelets usually 3-flowered, (2.8–)4.3–5.5 mm long; culm basal sheath bases slightly inflated, shiny, and tough; plants of more mesic puna; mostly 3700–4500 m……
..... *P.candamoana*
– Leaf blades flat or folded, somewhat lax, apex often tapered to a long slender point; spikelets 3–6 flowered, (5–)6–7.2 mm long; culm basal sheaths not as above; plants of more arid zones between 3000 and 4000 m elevation (appears to hybridise with P. kurtzii where the two overlap) . ..... *P.grisebachii*

27 (23). Leaf blades filiform or slightly broader, involute or subinvolute towards the base, 0.5–2 mm wide when expanded; lower lemma 3–4 (5?) mm long, glabrous; web only (web sometimes v. short and sparse, and present on basal florets only) ..... *P.pauciflora*
– Leaf blades flat or folded, usually >2 mm wide when expanded; lower lemma 2.3–6 mm long, variously glabrous or pubescent 28

28 (27). Basal sheaths glabrous and densely scabrous; lemmas smooth, glabrous; web only.
..... *P.scabrivaginata*
– Basal sheaths glabrous or lightly pubescent, smooth or lightly scabrous, or if densely scabrous then lemmas pubescent at least on the keel; lemmas smooth or scabrous, glabrous or pubescent in part 29

29 (28). Upper ligules 0.9–2(–3) mm long, truncate; plants distinctly rhizomatous; lower sheaths smooth, sometimes lightly pubescent; lower lemma keel and marginal veins distinctly pubescent; spikelets with 2–6 florets; all florets of spikelets hermaphroditic (sometimes anthers aborted late in development) ..... *P.pratensis*
– Combination of characters not as above; upper ligules 0.2–10 mm long, acute or rarely truncate; plants tufted (weakly rhizomatous in *P.huancavelicae* and cataphyllous psuedostolons present in *P.leioclada*); lower sheaths smooth to densely scabrous; spikelets with 2–3(–4) florets; upper floret within spikelets sometimes pistillate, with rudimentary stamens……. 30

30 (29). Leaf blades folded, apex prominently naviculate (prow-tipped); plants weakly rhizomatous; lemma keels and marginal veins smooth or asperulous, glabrous; web only……..*P.huancavelicae*
– Leaf blades flat, apex not, or not prominently, naviculate; plants tufted, occasionally stooling and rooting at nodes (cataphyllous psuedostolon present at the base in *P.leioclada*); lemma keels short pubescent in the lower ½, sometimes sparingly so on the marginal veins near the base 31

31 (30). Spikelets glomerate on branches; culm leaf ligules 1–2(–2.5) mm long, truncate or obtuse; a psuedostolon usually present at the base of the plant; spikelet proximal lemmas pubescent on keel, lateral, and marginal veins; distal lemmas often pubescent between the veins; spikelets 2–4 flowered; sheaths smooth; leaf blades mostly conduplicate, sometimes flat, firm; lowest floret of spikelets hermaphroditic, upper florets commonly pistillate *P.*cf. *leioclada*
– Spikelets diffuse throughout the panicle; culm leaf ligules 4–10 mm long, acute or rarely truncate; psuedostolons absent; spikelet proximal lemmas glabrous or sparingly pubescent on the keel, and sometimes marginal veins; distal lemmas often glabrous throughout; spikelets 2–3 flowered; sheaths nearly smooth to densely scabrous; leaf blades mostly flat, flaccid; all florets of spikelets hermaphroditic ..... *P.trivialis*

Checklist to the open-panicled *Poa* species of Peru

Poa aequatoriensis Hack. **Ref:** Standley (1936: 125); Tovar (1965: 45, 1993: 135). **Habitat:** Montane forest, puna grassland, pathsides and open areas, rocky slopes. 2000–4600 m. **Vouchers:** PERU: AMAZONAS: Bongara *J.J. Wurdack 944* (US). AYACHUCO: *Weberbauer 7573* (US fragm. Ex F). CAJAMARCA: Cajamarca *I. Sanchez Vega* (MO); San Miguel *J. Mostacero L. 1282* (MO); Santa Cruz *J. Santisteban C. 169* (F, MO). CUSCO: Urubamba *H.H.C. Ellenberg 48232* (MO). HUÁNUCO: Pachitea *J.F. Macbride 4365* (US). PIURA: Huancabamba *P.M.Peterson et al. 15175* (US). **Discussion:** Distributed through Ecuador and Peru, *P. aequitoriensis* occurs mostly from northern Peru to Colombia, although one collection is known from Cusco. Brako & Zarucchi (1993) and Tovar (1993) also state *P. aequatoriensis* to occur in the regións of ANCASH, HUANCAVELICA and LIMA, but specimens have not been verified by us. Commonly misidentified as *P. trivialis* and vice-versa. Reports of *P. aequitoriensis* from Bolivia by Hjorth (1991) are, most likely, another taxon. This report was probably based on material called *Poa umbrosa* Trinius (1830: 386) by Renvoize (1998; *Renvoize & Cope 4071*, K, US!), which RJS redetermined as *Poa bradei* Pilger (1935: 37), a species otherwise known only from Brazil, which has spikelets with purely perfect flowers and short anthers (0.5–1 mm).

Poa annua L. **Syn:** *Ochlopoa annua* (L.) H. Scholz. **Ref:** Standley (1936: 125); Tovar (1965: 61, 1993: 127). **Habitat:** Waste and disturbed ground, pathsides, roadsides and fields. 2200–4800 m. **Vouchers:** PERU: ANCASH: Carhuaz *D.N. Smith 9561* (MO); Huari *P.M. Peterson 13872* (MO, US); Huaylas *D.N. Smith 9294* (MO); Pallasca *P.M. Peterson 13947* (MO, US); Recuay *P.M. Peterson 13827* (MO, US). AREQUIPA: Arequipa *P.M. Peterson 18256* (US); Caraveli *P.M. Peterson 16391* (US). AYACUCHO: Huanca Sancos *P.M. Peterson 16258* (US); Lucanas *P.M. Peterson 16309* (US); Parinacochas *P.M. Peterson 16328* (US). CAJAMARCA: Cajamarca *P.M.*

Peterson 14910 (MO, US); San Ignacio *P.M. Peterson 15129* (MO, US). CUSCO: Calca *S.P. Sylvester 1334* (CUZ, LPB, US, Z); Canchis *J. Farfán 864* (MO); Cusco *P. Núñez V. 7500* (US); Espinar *P. Núñez V. 7619* (MO); La Convención *S.P. Sylvester 1552* (CUZ, US, Z). HUANCAVELICA: Huancavelica *P.M. Peterson 14173* (MO, US). JUNÍN: Junín *P.M. Peterson 14095* (MO, US); Tarma *D.N. Smith 1605* (MO). LA LIBERTAD: Bolivar *R.W. Bussmann 18047* (MO); Otuzco *A. Sagástegui A. 11567* (MO); Trujillo *J. Hudson 1027* (MO). PASCO: Oxapampa *D.N. Smith 5831* (MO). PUNO: Chucuito *P.M. Peterson 14634* (US); El Collao *P.M. Peterson 14593* (MO, US); Sandia *B.C. Bennett 1944* (MO). TACNA: Tarata *P.M. Peterson 14724* (MO, US). **Discussion:** Introduced weed from Europe. This species can occur with completely glabrous lemmas where it is commonly misidentified as *Poa supina* (see 'Species excluded' section below)**.** Brako & Zarucchi (1993) and Tovar (1993) also state *P. annua* to occur in the regións of HUÁNUCO, LIMA and PIURA, but specimens have not been verified by us.

Poa ayacuchensis Tovar **Ref:** Tovar (1974: 6, 1993: 129). **Habitat:** Wet ground, riversides. c. 3700 m. **Vouchers:** PERU: AYACUCHO: Lucanas *Ó. Tovar S. 7007* (MO, US). **Discussion:** Endemic herb, only known from the type collection.

Poa calycina (J. Presl) Kunth **Syn:** *Brizopyrum calycinum* J. Presl; *Deschampsia mathewsii* Ball; *Dissanthelium calycinum* (J. Presl) Hitchc.; *Dissanthelium laxifolium* Swallen & Tovar; *Dissanthelium mathewsii* (Ball) R.C. Foster & L.B. Sm.; *Dissanthelium sclerochloides* Steud. ex E. Fourn.; *Dissanthelium semitectum* Swallen & Tovar; *Dissanthelium supinum* Trin.. **Ref:** Refulio Rodríguez et al. (2012: 130); Swallen & Tovar (1965: 370–371); Tovar (1993: 154–156). **Habitat:** Puna grassland. 2500–4500 m. **Vouchers:** PERU: ANCASH: Bolognesi *P.M. Peterson 17974* (US); Recuay *P.M. Peterson 17904* (US); Yungay *P.M. Peterson 21676a* (US). AYACUCHO: Cangallo *P.M. Peterson 18164* (US); Lucanas *P.M. Peterson 16466* (US). CUSCO: Calca *P.M. Peterson 18100* (US); Urubamba *S.P. Sylvester 1706* (AAU, LPB, US). HUANCAVELICA: Huancavelica *P.M. Peterson 18100* (US). HUÁNUCO: Huamalies *P.M. Peterson 17923* (US). JUNÍN: Huancayo *P.M. Peterson 14209* (US); Junín *P.M. Peterson 14105* (US); Tarma *P.M. Peterson 14090* (US); Yauli *P.M. Peterson 18042* (US). LIMA: Canta *P.M. Peterson 18028* (US). PASCO: Pasco *P.M. Peterson 18075* (US). **Discussion:** This species has a disjunct distribution, being found in the high elevation puna grasslands of Bolivia and Peru and the alpine volcanic slopes of Mexico (Soreng & Peterson 2012). Brako & Zarucchi (1993) also state *P. calycina* to occur in the región PUNO, but specimens have not been verified by us.

Poa candamoana Pilg. (Nom. Cons. Prop. *In prep.*) **Syn:** *Poa adusta* J. Presl; *Poa pilgeri* Negritto & Anton. **Ref:** Standley (1936: 125); Tovar (1965: 57, 1993: 131); Negritto & Anton (2006: 87). **Habitat:** Grassland. 3400–4500 m. **Vouchers:** PERU: ANCASH: Pacllon *E. Cerrate 2685* (US); Recuay *P.M. Peterson 21547* (US); Yungay *P.M. Peterson 21748* (US). AREQUIPA: Arequipa *P.M. Peterson 18254* (US). AYACUCHO: Lucanas *H.H.C. Ellenberg 4945* (MO). CAJAMARCA: Celendin *P.M. Peterson 21915* (US). CUSCO: Cusco *A.S. Hitchcock 22469* (US); Espinar *C. Vargas C. 5629* (MO); Quispicanchis *P.M. Peterson 20599* (US). HUANCAVELICA: Huancavelica *P.M. Peterson 16422* (US); Churcampa *O. Tovar S. 805* (US); Huaytara *P.M. Peterson 20428a* (US); Tayacaja *O. Tovar S. 2475* (US). HUÁNUCO: Huamalies *P.M. Peterson 17925* (US). JUNÍN: Junín *P.M. Peterson 14116* (US); Huancayo *I.J. Blair 424* (K), *S. Soukup 6103* (US); Yauli *Hirsch P243* (US).

LIMA: Canta *P.M. Peterson 20286* (US). MOQUEGUA: Gral. Sanchez Cerro *D.B. Montesinos T. 2494* (MO, USM). PASCO: Pasco *P.M. Peterson 14099* (US). PUNO: *Azángaro A. Weberbauer 472* (MO, US); Puno *O.P. Pearson 52-68* (US). **Discussion:** A common element in the high Andean puna grassland of Peru and Bolivia. Brako & Zarucchi (1993) state *P. candamoana* to also occur in the región APURIMAC but specimens have not been verified by us. There has been large uncertainty regarding *Poa adusta,* which is known only from the type collection *Haenk s.n.* (PR, HAL). After studying the HAL isotype, it has been confirmed as *P. candamoana* and the type description of *P. adusta* can be considered erroneous regarding the lemma indumentum, which is stated to be scabrous whilst the specimen examined had pubescence present on the lemma veins. From studying digitized images of the PR isotype, this specimen appears to be a mixed collection with the left-hand plant conforming to *P. adusta* p.p. whilst the right-hand plant bears characteristics of *P. pratensis* and requires lectotipification. The origin of the *P. adusta* specimen is uncertain and the specimen may not have been collected from Peru, even though J. Presl (1830: 271) mentioned 'Peruvia' as place of origin in the protologue. The Haenke specimen was part of a bundle of specimens which were tagged with the note 'Aus verfault P.' written by Sternberg (translated as 'from rotten bundle'). This indicates that the specimen comes from a deteriorated bundle of plants, who's origin was probably unknown by Sternberg. Haenke's herbarium originally consisted of specimens without labels and, when the Berlin-Dahlem Museum purchased the bundle, the origin was indicated only on the top of every bundle of specimens. This is the reason why Haenke's handwriting is generally missing from all of his specimens. 'Peruvia', mentioned in the protologue, is therefore rather Presl's opinion about the origin of this species rather than the real place of origin and the species may come from any (suitable) place on the Pacific coast of America from Chile to Nootka (Otakar Sida (PR), *pers. communication*). Intermediate forms between *P. candamoana* and *P. horridula* have been found which may be the result of hybridisation (see *P. horridula* discussion below).

Poa compressa L. **Ref:** Soreng & Peterson (2012: 31). **Habitat:** Cool-temperate, semi-shaded to open habitats on wet ground. **Vouchers:** PERU: JUNÍN: Corpacancha *G.A. Sullivan 828* (MO). **Discussion:** Introduced weed, this species was introduced to the Neotropics for soil stabilization. Originating in Europe, it has since become naturalized in North America, Asia, Central and South America. This species usually has a congested inflorescence but infrequently exhibits an open inflorescence.

Poa fibrifera Pilg. **Syn:** *Poa carazensis* Pilg.; *Poa ferreyrae* Tovar; *Poa geniculata* Tovar; *Poa tovarii* Soreng. **Ref:** Standley (1936: 126); Tovar (1965: 37–44, 1984: 8, 1993: 128–130); Soreng (1998: 200). **Habitat:** Montane forest, puna grassland, rocky slopes. 2500–4500 m. **Vouchers:** PERU: ANCASH: Aquia *E. Cerrate 1577* (US); Bolognesi *E. Cerrate 2607* (US); Carhuaz *D.N. Smith 9493* (MO); Huaraz *D.N. Smith 10940* (MO); Huari *D.N. Smith 12590* (MO); Huaylas *D.N. Smith 9774* (MO); Pallasca *P.M. Peterson 13949* (US); Recuay *P.M. Peterson 13800* (MO, US); Santa *A. Weberbauer 3073* (MO, US); Ticllos *E. Cerrate 2650* (US); Yungay *P.M. Peterson 21741* (US). AYACUCHO: Lucanas *P.M. Peterson 18210* (US). CAJAMARCA: Cajamarca *I. M. Sánchez V. 3534* (MO); Celendin *I. M. Sánchez V. 3488* (MO); Contumaza *A. Sagástegui 9647* (MO); Hualgayoc *P.M. Peterson 14941* (MO, US). HUANCAVELICA: Huaytara *P.M. Peterson 18160* (US). LA LIBERTAD: Contumaza *E.S. Anderson 1265* (US); Otuzco *R. Ferreyra 7619* (MO, US); Santiago de

Chuco *A. Sagástegui A. 11809* (MO). LIMA: Canta *P.M. Peterson 20262* (US); Huarochiri *R. Ferreyra 8252* (US). **Discussion:** Endemic herb (a voucher from Bolivia, *T. Johns 82-108*, was redetermined by RJS as *P. horridula*). *Poa ferreyrae* and *P. geniculata* (=*P. tovarii*), known only from the type collections at La Libertad-Otuzco, and *P. carazensis*, known from the departamento of Ancash, are seen to be indistinct from *P. fibrifera* and so have been placed as synonyms of this species. Brako & Zarucchi (1993) also state *P. fibrifera* to occur in the región of JUNÍN and HUÁNUCO but specimens have not been verified by us. Specimens from JUNÍN originally identified as *P. fibrifera* (*A.S. Hitchcock 22176*; *P.M. Peterson 14227*) have been redetermined as *P. glaberrima* and *P. kurtzii*, respectively. It is impossible to say if either of these specimens were accepted by Brako & Zarucchi (1993) as only one specimen was cited for the country.

Poa gilgiana Pilg. **Syn:** *Melica expansa* Steud. ex Lechl.. **Ref:** Standley (1936: 126); Tovar (1965: 36, 1993: 128). **Habitat:** Grassland. 3700–4700 m. **Vouchers:** PERU: AREQUIPA: Arequipa *P.M. Peterson 18255* (US); Caraveli *P.M. Peterson 16394* (US). JUNÍN: Junín *A.S. Hitchcock 22251* (US). LIMA: Canta *P.M. Peterson 18025* (US). PUNO: *Azángaro A. Weberbauer 477* (MO, US); Chucuito *P.M. Peterson 14678* (US). TACNA: Tarata *P.M. Peterson 14830* (MO, US). **Discussion:** Distributed in high elevation puna grasslands from central Peru to Bolivia. Possibly a variety of *P. horridula* which needs further study. This species is suspected to hybridise with *P. horridula* with intermediate forms being collected from ANCASH-Aquia (*E. Cerrate 1564* (US)), HUANCAVELICA-Huaytara (*P.M. Peterson 20424a* (US)) and PUNO-Chucuito (*P.M. Peterson 14669* (MO, US)).

Poa glaberrima Tovar **Ref:** Tovar (1965: 40, 1993: 129). **Habitat:** Puna tussock grassland, humid areas, wet ground. 3300–4700 m. **Vouchers:** PERU: ANCASH: Recuay *P.M. Peterson 13821* (MO, US). APURIMAC: Ayamaraes *P.M. Peterson 16507* (US). AYACUCHO: Huamanga *P.M. Peterson 20532a* (US). CUSCO: Calca *P.M. Peterson 16555* (US). HUANCAVELICA: Huancavelica *P.M. Peterson 14168* (MO, US). JUNÍN: Huancayo *Anonymous 34* (US); Junín *D.N. Smith 5649* (MO); Tarma *D.N. Smith 2989* (MO); Yauli *P.M. Peterson 14044* (US). LIMA: Canta *P.M. Peterson 20282* (US); Huarochiri *J.R. Swallen 7068* (US). PUNO: Lampa *P.M. Peterson 20744* (US); Melgar *P.M. Peterson 20721* (US); Puno *H.H.C. Ellenberg 249* (US). **Discussion:** Previously considered an endemic herb but the species has been stated to occur in Ecuador, Bolivia and Argentina according to Giussani et al. (2012: 304), although specimens have only been verified from Bolivia (*S.A Renvoize 4475* [US]) by us. This species superficially resembles *P. candamoana* but the latter prefers dry ground and has hairy lemmas. Certain specimens placed under this name from southern Peru (eg. PUNO: Lampa “2 km SW of San Jose on road towards Junin” *P.M. Peterson 20744,* [US]; Melgar “ca. 7 km WNW of Santa Rosa on Hwy 3 and 1 km W toward Quishuara, along Rio Santa Rosa” *P.M. Peterson 20624b* [US]), Bolivia and northern Argentina (*P.M. Peterson* 19577 [US]; Giussani et al. 2012, Figure pg. 304) have odd forms with sparse inflorescences and may actually be a species new to science. They resemble *P. pauciflora,* but with completely glabrous and smooth spikelets. Future study should focus on verifying the species status of these southern *P. glaberrima* specimens.

Poa grisebachii R.E. Fr. **Syn:** *Poa superata* Hack.. **Ref:** Giussani et al. (2012: 305, 336). **Habitat:** Dry puna grasslands and high Andean steppe. 3000–4500 m. **Vouchers:** PERU: AYACUCHO: Parinacochas *P.M. Peterson 16323* (US). JUNÍN: Yauli *Ó. Tovar S. 6447* (MO). MOQUEGUA: Carumas *A. Weberbauer 7310* (US); Mariscal Nieto *P.M. Peterson 14553* (US). TACNA: Tarata *P.M. Peterson 14793* (MO, US). **Discussion:** Collections verified from Peru, Chile and Argentina. Previously, *P. grisebachii* and *P. superata* were both considered endemic to Argentina (Giussani et al. 2012) but this is the first recording of the species from Peru. It is likely that, with further revision of Bolivian *Poa*, this species will also be found to occur in Bolivia. Specimens of *P. grisebachii* and *P. superata* were found to be morphologically indistinct and so have been grouped as a single taxon. Certain specimens were found from AYACUCHO: Lucanas, e.g. *P.M. Peterson 16317* (US), that bore characteristics of *P. horridula*. Another specimen from MOQUEGUA: Mariscal Nieto *P.M. Peterson 14553* (US), could also not be confidently placed to the species. *Poa grisebachii* can, potentially, be highly variable in terms of lemma pubescence. The lectotype of *P. grisebachii* p.p. has glabrous and smooth lemmas whilst the isolectotype and other isosyntypes of *P. grisebachii* p.p. at US (fragms. ex UPS), and the type specimens of *P. superata* p.p., were all observed with pubescent lemmas. All Peruvian material of *P. grisebachii* has pubescent lemmas, at least for the distal florets. The plants resemble *P. fibrifera*, and are sometimes fibrous at their bases, but can usually be distinguished by the distinctly pubescent lemmas. The leaf blades are usually somewhat thin, flat, lax, and scabrous, 1.5–3.5 mm wide. This species may also hybridise with *P. kurtzii*, with intermediate forms being collected which exhibit narrower, firmer, involute blades and generally smaller spikelets.

Poa horridula Pilg. **Syn:** *Melica expansa* Steud ex Lechl.; *Poa dumetorum* Hack.; *Poa piifontii* J. Fernandez Casas, J. Molero & A. Susanna; *Poa pufontii* Fern. Casas, Molero & Susanna; *Poa unduavensis* Hack.. **Ref:** Standley (1936: 127); Tovar (1965: 53, 1993: 131). **Habitat:** Grasslands, rocky slopes, shrublands. 2900–4700 m. **Vouchers:** PERU: ANCASH: Bolognesi *P.M. Peterson 17888* (US); Pallasca *P.M. Peterson 21810* (US); Recuay *P.M. Peterson 13841* (MO, US); Santa *A. Weberbauer 3113* (MO, US); Yungay *P.M. Peterson 21631* (US). APURIMAC: Abancay *P.M. Peterson 16645* (US); Aymaraes *P.M. Peterson 16477* (US). AREQUIPA: Caylloma *P.M. Peterson 18298* (US). AYACUCHO: Huamanga *P.M. Peterson 20503* (US); Huanca Sancos *P.M. Peterson 16283* (US); Lucanas *P.M. Peterson 16289* (US); Parinacochas *P.M. Peterson 16346* (US). CAJAMARCA: Cajamarca *I.M. Sánchez V. 79* (US); Celendin *I.M. Sánchez V. 2911* (MO); Hualgayoc *P.M. Peterson 14938* (US). CUSCO: Anta *G.R. Brunel 283* (MO); Calca *S.P. Sylvester 1021* (CUZ, US, Z); Cusco *A.S. Hitchcock 22443* (US); La Convención *S.P. Sylvester 2028* (LPB, US, Z); Paruro *P. Núñez V. 7365* (MO); Quispicanchis *P.M. Peterson 20549* (US); Urubamba *H.H.C. Ellenberg 4824* (MO). HUANCAVELICA: Huancavelica *P.M. Peterson 14175* (MO, US); Huaytara *P.M. Peterson 18158* (US); Tayacaja *O. Tovar S. 4213* (MO). HUÁNUCO: Huamalies *P.M. Peterson 17922* (US); Yarowilca *J.F. Macbride 1970* (US). JUNÍN: Huancayo *Black 46-711* (US); Jauja *P.M. Peterson 14122* (US); Junín *A.S. Hitchcock 22213* (US). LA LIBERTAD: Bolivar *P.M. Peterson 21944* (US). LIMA: Canta *P.M. Peterson 20278* (US); Huarochiri *P.M. Peterson 14018* (MO, US); Yauyos *E. Cerrate 1083* (US). PASCO: Daniel Alcides Carrión *A.S. Hitchcock 22302* (US); Pasco *A.S. Hitchcock 22260bis* (US). PUNO: Chucuito *P.M. Peterson 14672* (US); Puno *H.H.C. Ellenberg 342* (US); Sandia *B.C. Bennett 2323* (MO). **Discussion:** Found above 3000 m in puna and paramo grasslands from Colombia to Bolivia. Brako & Zarucchi (1993) and Tovar (1993) also

state *P. horridula* to occur in the región of MOQUEGUA but specimens have not been verified by us. This species is suspected to hybridise with *P. gilgiana* (see *P. gilgiana* discussion, above) and *P. candamoana* due to the presence of intermediate forms across the ranges of these species. Specimens *Hirsch P1399* (US) and *E. Cerrate 2285* (US) appear to be intermediates between *P. horridula* and *P. candamoana* and could be either a short *P. horridula* or a robust *P. candamoana*.

Poa huancavelicae Tovar **Syn:** *Poa paramoensis* Lægaard. **Ref:** Tovar (1965: 52, 1993: 134); Lægaard (1998: 28). **Habitat:** Puna grassland and *Polylepis* woodland. 4000–4800 m. **Vouchers:** PERU: ANCASH: Bolognesi *P.M. Peterson 17953* (US); Huaraz *D.N. Smith 10839* (MO); Recuay *P.M. Peterson 21540* (US); Yungay *P.M. Peterson 21766* (US). CUSCO: Calca *P.M. Peterson 16604* (US); Carhuaz *D.N. Smith 11206* (MO); La Convención *S.P. Sylvester 1565* (US, Z); Quispicanchis *P.M. Peterson 20589* (US); Urubamba *H.H.C. Ellenberg 449* (MO). HUANCAVELICA: Castrovirreyna *Ó. Tovar S. 28* (MO). **Discussion:** Previously considered endemic to Peru and found in the regions HUANCAVELICA and CUSCO (Brako & Zarucchi 1993; Tovar 1993). *Poa paramoensis* was found to be inconsistently morphologically distinct from *P. huancavelicae*; the northern plants branches are usually fairly smooth, but the variation appears to be continuous to more scabrous forms further south in Peru, and so it has been sunk within this species. Specimens from La Convención, CUSCO, have proximal lemmas much shorter (3–3.5 mm) than in the original species description (4–4.5 mm) and anthers were also much shorter (1–1.3 mm). These plants were also found to be rhizomatous, whilst *P. paramoensis* p.p. is tufted and the isotype material of *P. huancavelicae* p.p. at MO appears tufted (although Tovar [1993] mentions it to be rhizomatous!!).

Poa infirma Kunth **Syn:** *Catabrosa thomsonii* Hook. f.; *Colpodium thomsonii* (Hook. f.) Hack.; *Eragrostis infirma* (Kunth) Steud.; *Megastachya infirma* (Kunth) Roem. & Schult.; *Ochlopoa infirma* (Kunth) H. Scholz; *Poa annua* subsp. *exilis* (Tomm. ex Freyn) Asch. & Graebn.; *Poa exilis* (Tomm. ex Freyn) Murb.; *Poa remotiflora* (Hack.) Murb.. **Ref:** Müller et al. (1981: 334); Tovar (1986: 56; 1993: 126). **Habitat:** Dry forest, puna grassland. c.4400 m. **Vouchers:** PERU: CUSCO: Calca *P. Núñez V. 7063* (MO), *S.P. Sylvester 1390* (US, Z). **Discussion:** Introduced from Europe. Brako & Zarucchi (1993) and Tovar (1993) state *P. infirma* to also occur in the regións of HUANCAVELICA and LIMA, with the specimens from LIMA being found on coastal hills in sandy soil, but specimens have not been verified by us.

Poa kurtzii R.E. Fr. **Syn:** *Poa altoperuana* R. Lara & Fern. Casas; *Poa asperiflora* Hack.; *Poa munozensis* Hack.; *Poa pflanzii* Pilg.. **Ref:** Standley (1936: 125); Tovar (1965: 60, 1993: 133); Giussani et al. (2012: 312). **Habitat:** High Andean puna grassland, rocky slopes. 3300–5100 m. **Vouchers:** PERU: ANCASH: Huari *D.N. Smith 10138* (MO); Recuay *P.M. Peterson 21510* (US). AREQUIPA: Arequipa *P.M. Peterson 18260* (US); Caraveli *P.M. Peterson 16393* (US). AYACUCHO: Huamanga *P.M. Peterson 20531* (US); Huanca Sancos *P.M. Peterson 16244* (US); Lucanas *P.M. Peterson 16177* (US); Parinacochas *P.M. Peterson 16345* (US). HUANCAVELICA: Castrovirreina *O. Tovar S. 2838* (US); Huancavelica *P.M. Peterson 16416* (US); Huaytara *P.M. Peterson 20426* (US). JUNÍN: Huancayo *P.M. Peterson 14227* (US). LA LIBERTAD: Trujillo *H.H.C. Ellenberg 3779* (MO). MOQUEGUA: Mariscal Nieto *P.M. Peterson 14552* (US), *P.M. Peterson 18312* (US). PUNO:

Azángaro *H.H.C. Ellenberg 598* (US); Chucuito *P.M. Peterson 14677* (US); El Collao *P.M. Peterson 14591* (US). TACNA: Tacna *P.M. Peterson 14762* (US); Tarata *P.M. Peterson 14727* (US). **Discussion:** This species is found from Peru to Argentina. JUNÍN specimen *P.M. Peterson 14227* is atypical and requires further study. Brako & Zarucchi (1993) state *P. asperifolia (=kurtzii)* to also occur in the regións CUSCO and LIMA but specimens have not been verified by us. The species is highly variable in terms of lemma indumentum and scabrocity, and has been keyed out twice in both keys (see Appendix 1) to account for this.

Poa cf. ***leioclada*** Hack. **Ref:** Hitchcock (1927) Habitat**:** Humid paramo grasslands. 3200–4300 m. **Vouchers:** PERU: ANCASH: Yungay *D.N. Smith 9095* (MO); Huaylas *D.N. Smith 9320a* (MO). PIURA: Huancabamba *P.M. Peterson 15175* (US). **Discussion:** Specimens are an imperfect match of Ecuadorian material of *Poa leioclada* as they bear characteristics of both *Poa mulalensis* Kunth and *P. leioclada*. Both these species were previously considered Ecuadorian endemics. This taxon needs further study.

Poa oscariana Negritto & Anton **Ref:** Negritto & Anton (2006: 84). **Habitat:** Puna grassland, rocky slopes. 3600–4100 m. **Discussion:** Endemic herb, only known from CUSCO, Paucartambo. None of the type or paratype specimens have been examined. This may be a variety of *Poa gilgiana* but further collections and study are needed before this can be verified.

Poa pauciflora Roem. & Schult. **Syn:** *Poa depauperata* Kunth; *Poa pardoana* Pilg.. **Ref:** Standley (1936: 128); Tovar (1965: 49, 1993: 133). **Habitat:** Puna grassland, rocky slopes. 3200–4900 m. **Vouchers:** PERU: ANCASH: Corongo *P.M. Peterson 21777* (US); Huaraz *D.N. Smith 10797* (MO); Huari *P.M. Peterson 13885* (MO, US); Huaylas *D.N. Smith 9930* (MO); Pallasca *P.M. Peterson 21842* (US); Recuay *P.M. Peterson 13848* (MO, US); Yungay *P.M. Peterson 21678* (US). CAJAMARCA: Cajamarca *P.M. Peterson 14887* (US), *H.H.C. Ellenberg 1825* (US); Celendin *P.M. Peterson 21905* (US); San Miguel *P.M. Peterson 14933* (US); San Pablo *P.M. Peterson 14878* (US). JUNÍN: Tarma *P.M. Peterson 14065* (US). LA LIBERTAD: Bolivar *P.M. Peterson 21936* (US); Sanchez Carrion *D.N. Smith 2242* (MO); Santiago de Chuco *P.M. Peterson 13953* (US). SAN MARTÍN: Mariscal Caceres *B. León 1654* (MO). **Discussion:** Specimens have also been verified from Ecuador but it is unclear whether this species extends to Colombia and Bolivia.

Poa pearsonii Reeder **Ref:** Tovar (1965: 33, 1993: 127); Giussani et al. (2012: 325). **Habitat:** Rocky puna grassland. 4500–4900 m. **Vouchers:** PERU: PUNO: El Collao *O.P. Pearson 91* (US). TACNA: Tacna *P.M. Peterson 13953* (MO, US). **Discussion:** Found from southern Peru, through Bolivia to Argentina. Brako & Zarucchi (1993) state *P. pearsonii* to also occur in the regions of LIMA and AREQUIPA but specimens have not been verified by us.

Poa pratensis L. **Ref:** Standley (1936: 128); Tovar (1993: 135); Giussani et al. (2012: 328). **Habitat:** Open Andean grasslands. 3500–3900 m. **Vouchers:** PERU: CAJAMARCA: Cajamarca *I.M. Sánchez V. 2668* (MO); San Miguel *P.M. Peterson 14921* (MO, US). HUANCAVELICA: Huancavelica *P.M. Peterson 18107* (US). JUNÍN: Huancayo *P.M. Peterson 14223* (US); Yauli *D.N. Smith 2979* (MO). **Discussion:** Introduced from Europe. Brako & Zarucchi (1993) state *P. pratensis* to also occur in the región PUNO but specimens have not been verified by us.

Poa ramifera Soreng & P.M. Peterson **Ref:** Soreng & Peterson (2010: 587). **Habitat:** Shrublands. 2700–3100 m. **Vouchers:** PERU: ANCASH: Corongo *P.M. Peterson 21804* (MO, US, USM). **Discussion:** Endemic herb, known only from the type locality.

Poa scabrivaginata Tovar **Ref:** Tovar (1965: 48, 1993: 134). **Habitat:** Shrublands. 2700–3100 m. **Vouchers:** PERU: CAJAMARCA: Santa Cruz *J. Santistaban C. & J. Guevara B. 169* (MO). HUÁNUCO: Pachitea *J.F. Macbride 4354* (MO, US). JUNÍN: Concepción *J.F. Macbride 3363* (US). **Discussion:** Endemic herb. Previously known only from the type collection from HUÁNUCO, further specimens has been discovered from CAJAMARCA and JUNÍN. This taxon is might be included in *P. aequatoriensis* as the range of variation in characters stated to distinguish them (more densely scabrous basal sheaths, longer ligules and lemmas), was found to sometimes overlap now that more material has been reviewed from Peru. However, the proximal lemmas are longer (4.2–5 mm), and the anthers range from 1.2–2 mm long.

Poa swallenii Refulio **Syn:** *Dissanthelium expansum* Swallen & Tovar. **Ref:** Refulio Rodríguez et al. (2012: 130); Swallen & Tovar (1965: 375); Tovar 1993: 157). **Habitat:** Puna grasslands. 3600-4600 m. **Vouchers:** PERU: CUSCO: Calca *P.M. Peterson 16594* (US), *P.M. Peterson 16569* (US), *P.M. Peterson 16612* (US); La Convención *O.F. Cook 1305* (US), *S.P. Sylvester 1924* (US, USM, Z); Urubamba *S.P. Sylvester 1071* (CUZ, US, Z). **Discussion:** Endemic herb. Swallen & Tovar (1965) and Tovar (1993) also cited *Macbride & Featherstone 2183* from HUÁNUCO, and *P.C. Hutchison 1215* from LIMA, but these specimens have not been verified by us.

Poa trivialis L. subsp. trivialis **Ref:** Standley (1936: 129); Tovar (1993: 134); Giussani et al. (2012: 336). **Habitat:** Andean slopes at middle elevations. **Vouchers:** PERU: JUNÍN: *A.S. Hitchcock 22277* (US)*, A.S. Hitchcock 22279* (US)*, A.S. Hitchcock 22266a* (US). **Discussion:** Introduced from Europe. Brako & Zarucchi (1993) state *P. trivialis* to also occur in the región CAJAMARCA but the cited specimen, *J. Mostacero L. 1282* (MO), has been redetermined as *P. aequatoriensis*. *P. trivialis* and *P. aequatoriensis* bear many superficial resemblances and can be easily confused. Hitchcock specimens had no habitat type or specific locality mentioned.

Poa trollii (Pilg.) Refulio **Syn:** *Dissanthelium trollii* Pilg.. **Ref:** Tovar (1986: 51; 1993: 153). **Habitat:** Dry puna grassland. 4400–4800 m. **Vouchers:** PERU: PUNO: El Collao *P.M. Peterson 18303* (US). **Discussion:** Distributed in the high Andean dry puna grassland between southern Peru and the Potosi department in Bolivia. This species normally has congested, spike-like panicles but can have open panicles during anthesis, which is why it was included in this treatment.

Newly described species

Poa ramoniana* Soreng & S.P. Sylvester*, sp. nov.

Type:—PERU. Región JUNÍN. Prov. Junín: Distr. Carhuamayo, orillas de la laguna de Capillacocha, {est. vicinity: S10.86443º W75.99256º} entre Carhuamayo y Paucartambo, puna grassland, 4200–4300 m, 8 Jan 1949, *R. Ferreyra 5200 p.p. a* (holotype US-2207173!, isotype: USM p.p.)

Plants gynomonoeious. **Perennials**; Rhizomatous, with well developed, slender, lateral tending, rhizomes, small tufted. **Tillers** extravaginal. **Culms** ca. 5 cm tall, erect, unbranched, isolated or two together; Culm nodes 1–2(–3), terete, smooth, included in the sheaths; Culm internodes less than 1 cm long (peduncle ca. 3 cm), terete, smooth. **Leaves** mostly basal; Sheaths slightly laterally compressed, keeled, smooth, glabrous; Butt sheaths papery or slightly fibrous in age; Uppermost culm sheath ca. 18 mm long, margins fused ca. 40% their length, distal sheaths longer than their blades; Collars and throats smooth, glabrous; Ligules 1–1.5 mm long, sometimes with a central dent to 2 mm long, indistinctly decurrent, abaxially moderately densely scabrous, apices obtuse, margin irregular sometimes with a tooth, of sterile shoots similar to those of the culm; Cauline blades to 2 cm long, mostly folded or infrequently flat, with strongly inrolled margins, abaxially, marginally, and adaxially smooth, glabrous, tips distinctly prow shaped; Blades graduated up the culm, the sub-terminal one the longest; Sterile shoot blades to 4.5 cm long. **Panicles** 2–2.5 cm long, open, exerted, ca. 1 cm wide, with 13–15 spikelets, proximal internode ca. 6 mm long, weakly scabrous angled; Rachis with 1 branch per node; Primary branches spreading to reflexed, the upper ones ascending, distinctly angled, closely scabrous along the angles; Lateral pedicels less than 0.5 mm long, scabrous angled; Longest branches ca. 7 mm, with 4–5 spikelets clustered in the distal half. **Spikelets** 3.5–4 mm long, ca. 1.5 x longer than wide, broadly ovate, laterally compressed, not bulbiferous, anthocyanic and bronzy; Florets (2–)3, the proximal 1 (or 2 if 3 total) perfect, the distal 1 pistillate; Rachilla internodes terete, distal internodes terete, 0.4–0.8 mm long, smooth, glabrous, mostly hidden; Glumes more or less equal, both broadly lanceolate, or the first lanceolate, sub-lustrous in the scareous-hyaline margins, distinctly keeled, keels smooth or distally sparsely scaberulous, apices acute and pointed to obtuse and blunt and denticulate; Lower glumes 2.5–3 mm long, 1-veined; Upper glumes 3–3.2 mm long, ca. 2 x wider than the lower, 3-veined; Calluses glabrous; Lemmas (the lowest) 2.9–3.5, 5-veined, broadly lanceolate to ovate, green proximally, anthocyanic distally with a wide bronzy band apically, strongly laterally compressed, distinctly keeled, thin, keel smooth or scaberulous distally, mostly smooth elsewhere, glabrous, intermediate veins distinct, not extending into the scarious apical margin, edges smooth, apices scarious-hyaline bronzy for the distal ca. 1 mm, edges smooth or slightly erose to denticulate, obtuse, blunt or slightly pointed; Paleas to 1 mm shorter than the lemma, glabrous, keels smooth or distally sparsely scaberulous. **Flowers** chasmogamous; Lodicules not observed; Anthers ca. 2 mm long (vestigial in pistillate flowers). **Caryopses** unknown. 2*n* = unknown.

Distribution:—Only known from the single locality in the Junín province of the central Peruvian Andes.

Habitat:—Puna grassland, 4200–4300 m, in wet margins/shore of lakes, in moss.

Etymology:—The species is named in recognition of the eminent Peruvian botanist, Ramón Alejandro Ferreyra (1910—2005) who collected the type and paratype.

Conservation status:—Data insufficient.

Additional specimens examined:—PERU. Región JUNÍN. Prov. Junín: Distr. Carhuamayo, Capillacocha cerca a Carhuamayo, puna grassland, 4200–4300 m, 8 Jan 1949, *R. Ferreyra 5211* (USM!).

Discussion:—This new species appears like a small form of *P. glaberrima*, but differs by being extensively rhizomatous and reaching only 5 cm tall, versus densely tufted and 12—45 cm tall for *P. glaberrima*. The US holotype is a mixed collection, with a second taxon p.p. "b", which appears to be *Poa gymnantha* Pilger (1920: 28), that is sterile, tightly tufted, with intravaginally branching shoots and involute leaf blades that are adaxially scabrous. The USM isotype also contains two species: the small rhizomatous plant is *P. ramoniana*; the taller plants appear to be *P. glaberrima*. Tovar originally determined the USM type and paratype as *Poa lilloi* (Tovar 1993), which, among other differences, has a dense habit, without rhizomes, and ascending panicles branches, densely scabrous lemmas with narrow white, scarious margins, and sometimes a web on the callus. Tovar also identified the US type as *Poa ovata* Tovar (1965: 17), which RJS considers to be a rare to uncommon sexually reproducing phase of the small form of *P. gymnantha*, a species that is otherwise predominantly pistillate and apomictic (Negritto et al. 2008). Other material determined as *P. lilloi* in Peru has been referred to *P. glaberrima* and *P. candamoana*, or small *P. kurtzii* (see excluded species, below).

Poa tayacajaensis* Soreng & S.P. Sylvester, *sp. nov.

Type:—PERU: Región HUANCAVELICA. Prov. Tayacaja: Distr. Colcabamba, Chuspi-Hda., Tocas, entre Colcabamba y Paucarbamba, monte bajo, 2900 m, [vic. S 12.5º W 74.6º], 22 Apr 1954*, Ó. Tovar. S. 2038* (holotype: US-2181284!; isotypes USM)

Plants gynomonoecious. **Perennials**; tufted, without lateral or downward tending shoots. **Tillers** intravaginal. **Culms** 55–65 cm tall, erect or decumbent (when decumbent sometimes extravaginally branching at the lower culm nodes, i.e. *Peterson et al. 20369*); Culm nodes 3–4, terete, smooth, 2–3 nodes exposed at flowering; Culm internodes terete, smooth. **Leaves**; Sheaths slightly laterally compressed, keeled, lower culm and lateral ones densely scaberulous distally; Butt sheaths thin papery, somewhat loosely investing the shoots; Uppermost culm sheaths 10–13 cm long, margins fused 60–75 % their length, slightly shorter than their blades; Collars and throats smooth, glabrous; Ligules 2.0–3.5 mm long, not decurrent, abaxially sparsely to moderately densely scabrous, apices obtuse to subacute, margins densely asperous, ligules of sterile shoots and lower culm leaves 0.5–1 mm long; Cauline blades well developed, longer than their sheaths, 6–15 cm long, 3–5 mm wide, generally flat, keeled, thin, lax, abaxially, marginally, and adaxially scabrous mainly along the veins, folded near the apex, apex gradually tapered to a slender point; Blades gradually increasing in length up the culm, flag leaf blade 10–15 cm long; Sterile shoot blades like those of the culm, but somewhat shorter and smoother. **Panicles** 18–20 cm long, loose, open, exerted, slightly lax, to 5 cm wide, with more than 100 spikelets, proximal internodes 3.5–4 cm long, smooth; Rachis with (3) 5–6 branches at lower nodes; Primary branches slender, mostly laxly ascending, sometimes spreading, one sometimes reflexed, angled, proximally smooth to moderately scabrous mainly on the angles;

Lateral pedicels mostly < 1 mm long, scabrous; Longest branches 6–8 cm, with 14–22 spikelets in the distal half, slightly overlapping. **Spikelets** 4.5–6 mm long, ca. 2 x longer than wide, lanceolate, laterally compressed, not bulbiferous, greyish-green to somewhat anthocyanic at maturity; Florets (3–)4(–5), proximal florets hermaphroditic and distal one pistillate; Rachilla internodes terete, distal internodes terete, 0.7–1 mm long, smooth, glabrous; Glumes unequal, narrow lanceolate to lanceolate, herbaceous and pale green below, sometimes anthocyanic in margins and apex, veins distinct, distinctly keeled, keels sparsely short scabrous distally, surfaces smooth, margins scarious-hyaline, edges entire smooth, apices sharply acute, entire; Lower glumes 1.7–2.5 mm, 2/3–4/5 as long as adjacent lemmas, 1-veined, very narrow, slightly sickle shaped; Upper glume 2.4–3 mm, ca. 2 x wider than the lower, 3-veined; Calluses webbed, with a dense, long dorsal tuft of wooly hairs; Lemmas (the lowest) 2.8–3.7 mm long, 5-veined, lanceolate in side view, the proximal one ca. 5 x longer than wide at maturity, greyish-green, to strongly anthocyanic at maturity, strongly laterally compressed, distinctly keeled, thin, keel to 3/4 the length and marginal veins and sometimes the intermediate veins to 1/2 the length, loosely sericious to villous, between veins sparsely to moderately densely appressed pubescent or occasionally glabrous on the proximal lemma, keel distally weekly scabrous, intermediate veins distinct, not extending to near the margin, margins inrolling below at maturity, very narrowly hyaline above, edges smooth or with a few hooks, apices acute, briefly hyaline; Paleas shorter than the lemmas by ca. 0.5 mm, keels scabrous distally, sometimes weakly so, sparsely puberulent medially or nearly so, glabrous. **Flowers** chasmogamous; Lodicules ca. 0.25 mm long, obscurely lobed; Anthers 1.2–1.4 mm long, vestigial in the upper floret. **Caryopsis** 1.8–2 mm long, strongly laterally compressed, sulcate, honey brown, firm, adherent to the lemma and palea, hilum 0.2 mm long, elliptical. 2*n* = unknown.

Distribution:—Endemic to the central Andes of Peru. Known from Huancavelica and Huánuco, although the Huánuco specimen is only tentatively placed.

Habitat:—Shrublands on Andean slopes at mid elevations.

Etymology:—The name refers to the Peruvian province, Tayacaja, from where the type specimen was collected.

Conservation status:—Data insufficient.

Additional specimens examined:—Another specimen appears to represent this species but is too immature to be certain. The specimen in question has extravaginal shoots branching from lower culm nodes; PERU: Región HUÁNUCO. Prov. Pachitea: Distr. Chaggla, canyon of the Rio Grande, ca. 20 km above confluence with Rio Huallaga, E of Huánuco ca. 44 air km, 1.7 air km SSW of Estación Huacachay (Huacachi), 2650 m, S9.86836 W75.83306, 8 Mar 2007, *Peterson, Soreng & Romaschenko 20369* (US).

Discussion:—This species bears similarities to *Poa aequitoriensis* but differs by having lemmas which are generally shorter (2.8–3.7 mm long), pubescent between the veins, and by more densely scabrous sheaths, with more-or-less smooth glabrous throats, ligules generally shorter. Tovar (1993) placed the type of this new species in *P. aequitoriensis*. However, among the 20 sheets and the US isotype reviewed of *P. aequitoriensis*, all have lemmas that are smooth and glabrous between the veins (consistent with the description by Hjorth, 1991), and the keel and marginal veins can be glabrous or sparsely puberulent.

Poa urubambensis* S.P. Sylvester & Soreng, *sp. nov.

Type:—PERU. Región CUSCO. Prov. Calca: Distr. Calca, top of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán, 4401 m, S13° 16' 05.9" W72° 01' 17.2", 27 May 2011, *S.P. Sylvester 1317* (holotype USM!, isotypes CUZ!, K!, MO!, US!, Z!)

Plants gynomonoecious. **Perennials or (rarely) annuals**; Rhizomatous with well developed, slender, lateral tending, rhizomes, solitary and erect, or rarely tufted, often rooting from nodes. **Tillers** extravaginal. **Culms** (3–)15–30(–42) cm tall, decumbent to ascending, sometimes erect, fairly slender, not branching above the base, leafy; Culm nodes 1–2(–3), terete or slightly compressed, smooth, usually 1 node exposed at flowering; Culm internodes 3–15(–20) cm long, terete, smooth. **Leaves** mostly basal; Sheaths slightly compressed to keeled, smooth or scabrous along the veins; Butt sheaths papery, smooth, glabrous; Uppermost culm sheaths (3.5–)8–16 cm long, margins fused 25–60% the length, 1.8–2.7 × longer than their blades; Collars and throats smooth or scabrous, glabrous, collar margins of sterile shoot leaves sometimes flared; Ligules 1–4 mm long, not decurrent, scarious to hyaline, adaxially glabrous to scabrous, upper margins entire or irregularly dentate, apices acute and entire to irregularly dentate above, sterile shoot ligules generally shorter and more scabrous than those of the culm leaves; Cauline blades 2–15(–22) cm long, (1.5–)2–3 mm wide, flat or folded, margins often becoming involute, thin to moderately thin, soft or (rarely) curved, surfaces abaxially and adaxially lightly to moderately scabrous or rarely smooth, margins scabrous, narrowly to abruptly prow-tipped; Mid-cauline blades the longest, 10–22 cm long, shorter upward, flag leaf blade 3.5–7.7 cm long; Sterile shoot blades similar to cauline blades, sometimes more involute. **Panicles (**4–)8–13 cm long, erect, loosely contracted to open, ovoid to narrowly pyramidal, sparsely to moderately congested, with 13–40(–80) spikelets, proximal internode 1.4–3 cm long, smooth or scaberulous, usually scabrous towards its apex; Rachis with (1–)2–3(–5) branches per node; Primary branches ascending, fairly flexuous, weakly angled, moderately scabrous; Lateral pedicels mostly 3/4 to equaling the spikelets, moderately to densely scabrous, prickles moderately coarse; Longest branches 3–5 cm long, with 5–15 spikelets in distal 1/2, loosely arranged. **Spikelets** 3.7–6.5 mm long, to 3.7 × long as wide, lanceolate, laterally compressed, not bulbiferous, two toned; Florets 2–3(–4), proximal 1 or 2 florets hermaphroditic and distal 1 or 2 pistillate or sterile; Rachilla internodes terete, distal internodes terete, 0.6–1 mm long, smooth, glabrous; Glumes equal to subequal, narrow lanceolate, herbaceous and pale green below, scarious bronzy and sometimes anthocyanic in margins and apex, veins distinct, distinctly keeled, usually scabrous purely on the veins and sometimes between veins, margins scarious-hyaline, edges entire or dentate, smooth, apices acute, entire; Lower glumes 3.1–3.5 mm long, 2/3–4/5 as long as adjacent lemmas, 1-veined, narrow; Upper glumes 3.4–3.9 mm long, ca. 2 x wider than the lower, 3-veined; Calluses glabrous; Lemmas (the lowest) 3.2–3.9 mm long, 5-veined, lanceolate in side-view, the proximal one ca. 4–8 x longer than wide at maturity, proximally light green and distally bronzy-anthocyanic at maturity, moderately laterally compressed, thin, keeled, keels to 1/3–5/6 and marginal veins to 3/5–4/5, proximally smooth, keel and sides distally sparsely to moderately scaberulous, intermediate veins obscure to moderately prominent, not extending to near the margin, margins broadly scarious-hyaline, edges scabrous, apices acute; Paleas to 1.6 mm shorter than the lemma, glabrous, keels distally sparsely to moderately scabrous, between keels narrow (0.3–0.4 mm). **Flowers** chasmogamous;

Lodicules ca. 0.25 mm long, obscurely to shallowly lobed; Anthers 0.7–1.1(–1.3) mm long, infrequently vestigial in upper florets of spikelets. **Caryopses** ca.1.9 mm long, elliptical in side-view, sulcus broad and shallow, brown, hilum 0.2 mm long, oval, grain free from the palea. 2*n* = unknown.

Distribution:—Restricted to undisturbed areas of *Polylepis* woodland in hard to access areas throughout the Cordillera Urubamba, Cusco, Peru, at 4390-4802 m a.s.l.. Known from three localities; 1) Cliff ledges of the prominent SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán. 2) Ledges of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán. 3) Ridgeline to the W of Laguna Manalloqsa, Área de Conservación Privada (ACP) Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of Laguna Ipsaycocha.

Habitat:—Relatively dr*y* and exposed sites in montane *Polylepis* forest and forest edges.

Etymology:—The name 'urubambensis' refers to the Cordillera Urubamba, the mountain range where the species was collected from and which is seen from the closest town of Urubamba, situated at the valley bottom.

Conservation status:—This narrow endemic is locally common.

Additional specimens examined:—PERU. Región CUSCO. Prov. Calca: Distr. Calca, large ledge situated on the prominent SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4524 m, S13° 14' 35.1" W72° 01' 14.1", 21 March 2011, *S.P. Sylvester 812* (CUZ!, US!, Z!); Distr. Calca, large ledge situated on the prominent SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4517 m, S13° 14' 35.0" W72° 01' 13.7", 24 March 2011, *S.P. Sylvester 869* (CUZ!, US!, Z!); Distr. Calca, within the SW facing forest at the top of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán, 4390 m, S13° 16' 07.7" W72° 01' 16.8", 11 June 2012, *S.P. Sylvester 1636* (US!); Distr. Calca, within the SW facing forest at the top of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán, 4390 m, S13° 16' 07.7" W72° 01' 16.8", 11 June 2012, *S.P. Sylvester 1637* (CUZ!, SI!, US!, Z!); Distr. Calca, top of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán, 4401 m, S13° 16' 05.9" W72° 01' 17.2", 11 June 2012, *S.P. Sylvester 1695* (CUZ!, US!, Z!); Prov. Urubamba: Distr. Urubamba, ACP Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of Laguna Ipsaycocha, ledges on cliff side 250°W of Laguna Manalloqsa, 4676 m, S13° 12' 01.3" W72° 08' 47.4", 28 January 2011, *S.P. Sylvester 403* (CUZ!, US!); Distr. Urubamba, ACP Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of Laguna Ipsaycocha, topmost of the ridge to the W of Laguna Manalloqsa, 4802 m, S13° 12' 08.9" W72° 08' 43.9", 25 June 2012, *S.P. Sylvester 1727* (CUZ!, US!, Z!).

Discussion:—This new species is similar to members of *Poa* supersect. *Homalopoa* from Peru, Bolivia and Argentina, all of which have open panicles and spikelets with 2–5(–8) florets, the lowermost florets hermaphroditic whilst the upper florets are pistillate. *Poa urubambensis* is easily recognised in the field by the combination of an open-panicled inflorescence, glabrous lemmas and calluses, and exceptionally small anthers for members of *Poa* supersect. *Homalopoa*. *Poa urubambensis* also bears resemblance to *Poa oscariana* Negritto & Anton (2006: 84), but is distinguished by a less robust habit, the leaf blades being mainly basal and the anthers being smaller.

During fieldwork aimed at reconstructing the potential natural vegetation (PNV) and soils of the puna (see pilot studies by Sylvester et al. 2014 and Heitkamp et al. 2014), *Poa*

urubambensis was found to constitute an important part of the natural vegetation in the Cordillera Vilcanota, being found growing alongside other species new to science, e.g. *Bartsia lydiae* S.P. Sylvester (2014: 41). Following indicator species analyses, *Poa urubambensis* has been found as an indicator species for the PNV, due to its frequency and abundance within relict patches of near natural vegetation (Sylvester et al., *unpubl. data*). This species has not been found in accessible, disturbed or secondary, vegetation at similar or lower elevations in the Andes of the Cuzco region, despite a more thorough botanical exploration. This may relate to its susceptibility to disturbance from grazing and burning (Sylvester, *pers. observation*).

Species excluded

Poa androgyna Pilg. **Ref:** Renvoize (1998: 144). **Discussion:** *P. androgyna* has been described for Chile and Bolivia (Soreng et al. 2003 and onwards; Renvoize 1998) with Renvoize (1998) mentioning the species to occur in Peru but not citing specimens and none have been encountered so far. The name is difficult to apply and taxonomists are still unsure of what it is exactly. Past authors (Hitchcock 1927; Standley 1936; Foster 1958; Brako & Zarucchi 1993) have placed this name as a synonym of *P. horridula*, which is quite likely, but not certainly. Plants identified as *P. androgyna* have narrower leaf blades and more reflexed panicle branches than that typical of *P. horridula*.

Poa bromoides Vahl = ***Eragrostis bromoides*** (Vahl) Steud. **Ref:** Steudel (1854: 276). **Discussion:** Indiscrepancy centers around Brako & Zarucchi's (1993) inclusion of *P. bromoides* for Peru. As the type protologue of *Poa bromoides* states the plant to be cultivated: "Cult. Habitat (L)imae? Ex horto parisino habui" (Vahl 1794: 10), this effectively rules out the specimen being placed as *Poa*. Steudel's (1854) description also includes "spiculis lanceolatis 25-floris glabris" (pp. 276), i.e. spikelets lanceolate, 25-flowered, that places further doubt on the specimen belonging to *Poa*. Grassbase (Clayton et al. 2006 onwards) accepts *Poa bromoides* Vahl as *Eragrostis bromoides* (Vahl) Steud. {appl. uncert. but valid}.

Poa lilloi Hack. **Ref:** Tovar (1965: 32; 1993: 127); Giussani et al. (2012: 319). **Discussion:** Specimens of *P. lilloi* cited by Tovar (1993) to occur in Peru, *Ó. Tovar S. 2501* (US), *J.R. Swallen 7060b* (US) and *J.R. Swallen 7068* (US) have been redetermined as stunted versions of *P. glaberrima*. Specimen *J.R. Swallen 7060a* (US) was redetermined as a stunted version of *P. candamoana*. The specimen of *P. lilloi* from JUNÍN cited by Brako & Zarucchi (1993) and Tovar (1993), *R. Ferreyra 5260* (US, USM), has not been found. Neither has specimen *E. Cerrate 988* (USM?), cited by Tovar (1993) from JUNÍN, been verified. Certain specimens identified as *P. lilloi* may actually be the new species *Poa ramoniana*. The type of *P. ramoniana*, *R. Ferreyra 5200* (US, USM), was previously determined as *P. lilloi*, and the USM isotype appears as a mixed collection of *P. glaberrima* and *P. ramoniana*. It is the highly probable that all specimens previously considered as *P. lilloi* from Peru are stunted versions of either *P. candamoana*, *P. glaberrima* or *P. kurtzii* that were collected from heavily grazed areas or *P. ramoniana*. Correctly determined specimens of *P. lilloi* have been found from Bolivia, Chile and Argentina and occur in high elevation puna grasslands above c. 3200 m. This species is most easily confused with *P. kurtzii* from which it can be distinguished by being scabrous across the glume and lemma surface, sometimes with a bit of pubescence on the lemma keel, sometimes a tiny web

emerging from the dorsal side of the callus. *P. kurtzii*, on the other hand, has smooth glumes and densely scabrous lemmas. *P. kurtzii* is also gynomonecious whilst *P. lilloi* is gynodioecious.

Poa supina Schrader **Ref:** Tovar (1993: 126). **Discussion:** This taxon is highly unlikely to occur in South America with all specimens of *P. supina* so far encountered pertaining to *Poa annua*. These include all specimens so far encountered from Ecuador and Bolivia (Simon Laegaard *pers. communication*). Tovar (1993) includes *P. supina* in his treatment of Peru separating it from P. annua and P. infirma by having glabrous lemmas, or only lightly pubescent on the nerves, and swollen culms. However, the main distinction between *P. supina* and *P. annua* is in the size of the anthers with *P. supina* having anthers (1.2–)1.6–2(–2.5) mm long whilst *P. annua* has anthers 0.7–1.2 mm long. Specimens examined of *P. supina* from Peru (*J. Espinoza 2* (US)) were redetermined as *P. annua* but the voucher collections *Tovar & Rivas Martinez 7720* and *Tovar 7855* accepted by Tovar (1993) have not been seen by us.

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Appendix 1. SUPPLEMENTARY KEY TO THE OPEN-PANICLED SPECIES OF *POA* IN PERU

1. Glumes exceeding the distal florets; spikelets 2-flowered; lemmas 3 (rarely 5)-veined, glabrous, smooth or scaberulous; low tufted (sometimes rhizomatous in *P.trollii*) perennial plants mostly less than 10 cm tall; panicles 1–3.3 cm long 2
– Glumes shorter than the proximal floret; spikelets 2–4(–6)-flowered; lemmas 5(or 7)-veined, glabrous or pubescent, smooth or variously scabrous; annual or perennial plants of various habits, ranging mostly from 10–120 cm tall; panicles longer (sometimes short in the annuals) 4

2 (1). Anthers 2–2.2 mm long; lemmas smooth throughout; plants sometimes rhizomatous..... *P. trollii*
– Anthers <1 mm long; lemmas scaberulous, at least on the keels (rarely smooth in *P.calycina*); plants densely tufted 3

3 (2). Leaf blade abaxial surface shiny with leaf veins indistinct ..... *P.calycina*
– Leaf blade abaxial surface dull with leaf veins apparent ..... *P.swallenii*

4 (1). Culm nodes strongly compressed, lower culm nodes exposed; culms wiry; strongly rhizomatous with isolated shoots ..... *P.compressa*
– Combination of characters not as above; culm nodes terete or slightly compressed, lower culm nodes usually held within sheaths; culms varying from wiry to robust; tufted or rhizomatous 5

5 (4). Lemmas glabrous, smooth or scabrous (rarely sericeous at the base in *P.ramifera*); callus glabrous 6
– Lemmas, at least of the upper florets, pubescent or villous in their lower half (rarely glabrous in *P.annua*, scabrous-pubescent in *P.kurtzii*), or glabrous but then callus webbed, i.e. with long silky hairs emerging from below the lemma keel; callus glabrous or webbed 15

6 (5). Culms erect, aerially branching well up the culm with lateral shoots that persist and flower in subsequent seasons ..... *P.ramifera*
– Culms not branching, or branching only near the base, or from decumbent culms 7

7 (6). Lemmas surface usually completely smooth 8
– Lemmas slightly to strikingly scabrous between and on veins 11

8 (7). Plants 4–6 cm tall; rhizomatous; ligule <1 mm long ..... *P.ramoniana*
– Plants > 10 cm tall; tufted or, if rhizomatous > 100 cm tall; ligules 2–7 mm long 9

9 (8). Leaf blades smooth throughout, (2–)4–9 cm long, 1–2(–2.5) mm wide when blade flattened ..... *P.glaberrima*
–Leaf blades densely scabrous throughout, 8–40 cm long, 3–10 mm wide when blade flattened 10

10 (9). Leaf blades conspicuously conduplicate; plants 25–35 cm tall, tufted ..... *P.gilgiana*
– Leaf blades flat; plants 100–150 cm tall, rhizomatous ..... *P.ayacuchensis*

11(7). Anthers 0.7–1.1(–1.3) mm long; blades soft, thin and lax ..... *P.urubambensis*
– Anthers 1.8–3.2 mm long; blades firm to soft, thin and lax 12

12 (11). Leaf blades involute (rarely conduplicate in *P.kurtzii*), densely scabrous (at least abaxially), firm to rigid; plants tufted; ligule (2.5–)5–15 mm long 13
– Leaf blades flat or folded, rarely involute, glabrous or lightly scabrous, lax or firm; plants erect (*P. fibrifera*) or rhizomatous (*P. oscariana*), sometimes tufted; ligule 1–7(–9) mm long 14

13 (12). Ligule 8–15 mm long; panicles narrowly ovate, panicle branches ascending and subappressed, panicles included in the sheaths; lemmas scabrous ..... *P.pearsonii*
– Ligule (2.5–)5–8 mm long; panicles amply ovate, panicle branches patent or reflexed, panicles exerted; lemmas scabrous-pilose ..... *P.kurtzii*

14 (12). Lower leaf sheaths often fibrous; ligules 1.5–5(–6) mm long; blades lax; spikelets 3–5 flowered, 5–9 mm long; anthers 2.4–3.5 mm long; rachilla internodes well exposed ..... *P.fibrifera*
– Lower leaf sheaths not fibrous; ligules 6–9 mm long; blades somewhat firm; spikelets 2–3 flowered, 4.5–5 mm long; anthers 1.8-2 mm long; rachilla interrnodes short (compare with *P. gilgiana*)..... *P.oscariana*

15 (5). Plants annual; palea keels distinctly pubescent in part (very rarely glabrous) always without any hooks; web absent 16
– Plants perennial; palea keels glabrous or pubescent in part, but always scabrous in part; web absent or present 17

16 (15). Anthers 0.2–0.5(–0.6) mm long; panicle branches ascending, spikelets usually crowded; foliage light green; plants ephemeral ..... *P.infirma*
– Anthers 0.6–1 mm long; panicle branches ascending to spreading, spikelets loosely arranged; foliage usually darker green; plants infrequently persisting for more than one season ..... *P.annua*

17 (15). Callus glabrous; lemmas (at least the distal ones within a spikelet) softly villous-pubescent in their lower half 18
– Callus webbed, i.e. with long silky hairs (sometimes sparse) emerging from below the lemma keel (at least of the lower florets); lemmas glabrous or distinctly to sparsely villous or serious pubescent along the keel and marginal veins only 21

18 (17). Plants (30–)60–150 cm tall; Leaf blades flat, , sometimes folded towards their apices, usually more than 3 and up to 10 mm wide; inflorescence branches commonly verticillate; plants (sub-)rhizomatous with extravaginal shoots (if blades rather firm and folded but broad as in *P. horridula*, compare with *P. gilgiana*, possibly hybrids) ..... *P.horridula*
– Plants usually <35 cm tall; leaf blades involute to narrowly convolute and 0.5–2 mm wide, or flat to folded and 1–5 mm wide in *P.grisebachii*; inflorescence branches solitary or paired (often 3 branches in basal nodes of *P.grisebachii);* plants usually with only intravaginal shoots, (rarely sub-rhizomatous in *P.grisebachii)* 19

19 (18). Leaf blade abaxial surface densely scabrous; ligule (2.5–)5–8 mm long, acute; lemmas scabrous-pilose; plants of semi-arid habitats ..... *P.kurtzii*
–Leaf blade abaxial surface glabrous to scaberulous with prickles or hooks usually restricted to the leaf margin; ligule 0.5–3 mm long, truncate; lemmas pilose-villose towards base; plants of mesic or more arid habitats 20

20 (19). Leaf blades usually involute (no extravaginal shoots), apex narrowly but abruptly naviculate; spikelets usually 3-flowered, (2.8–)4.3–5.5 mm long; culm basal sheath bases slightly inflated, shiny, and tough; plants of more mesic puna; mostly 3700–4500 m ..... *P.candamoana*
– Leaf blades flat or folded, somewhat lax, apex often tapered to a long slender point; spikelets 3–6 flowered, (5–)6–7.2 mm long; culm basal sheaths not as above; plants of more arid zones between 3000 and 4000 m elevation (appears to hybridise with P. kurtzii where the two overlap) ..... *P.grisebachii*

21(17). Leaf blades filiform or slightly broader, involute or subinvolute towards the base, 0.5–2 mm wide when expanded; lower lemma 3–4 (5?) mm long, glabrous; web only (web sometimes v. short and sparse, and present on basal florets only) ..... *P.pauciflora*
– Leaf blades flat or folded, usually >2 mm wide when expanded; lower lemma 2.3–6 mm long, variously glabrous or pubescent 22

22 (21). Basal sheaths glabrous and densely scabrous; lemmas smooth, glabrous; web only ..... *P.scabrivaginata*
– Basal sheaths glabrous or lightly pubescent, smooth or lightly scabrous, or if densely scabrous then lemmas pubescent at least on the keel; lemmas smooth or scabrous, glabrous or pubescent in part 23

23 (22). Upper ligules 0.9–2(–3) mm long, truncate; plants distinctly rhizomatous; lower sheaths smooth, sometimes lightly pubescent; lower lemma keel and marginal veins distinctly pubescent; spikelets with 2–6 florets; all florets of spikelets hermaphroditic (sometimes anthers aborted late in development) ..... *P.pratensis*
– Combination of characters not as above; upper ligules 0.2–10 mm long, acute or rarely truncate; plants tufted (weakly rhizomatous in *P.huancavelicae* and cataphyllous psuedostolons present in *P.leioclada*); lower sheaths smooth to densely scabrous; spikelets with 2–3(–4) florets; upper floret within spikelets sometimes pistillate, with rudimentary stamens..... 24

24 (23). Leaf blades folded, apex prominently naviculate (prow-tipped); plants weakly rhizomatous; lemma keels and marginal veins smooth or asperulous, glabrous; web only ..... *P.huancavelicae*
– Leaf blades flat, apex not, or not prominently, naviculate; plants tufted, occasionally stooling and rooting at nodes (cataphyllous psuedostolon present at the base in *P.leioclada*); lemma keels short pubescent in the lower ½, sometimes sparingly so on the marginal veins near the base(rarely glabrous in *P.aequatoriensis*) 25

25 (24). Spikelets glomerate on branches; upper ligules 1–2(–2.5) mm long, truncate or obtuse; a psuedostolon usually present at the base of the plant; spikelets 2–4 flowered; lemmas 2.5–3.5 mm long; sheaths smooth; leaf blades mostly conduplicate, sometimes flat, firm..... *P.*cf. *leioclada*
– Spikelets diffuse throughout the panicle; upper ligules 1–10 mm long, acute or rarely truncate; psuedostolons absent; spikelets 2–3 flowered; lemmas 2–4 mm long; sheaths smooth or scabrous; leaf blades mostly flat, flaccid 26

26 (25). Spikelet proximal lemmas pubescent on keel, lateral, and marginal veins; distal lemmas pubescent between the veins; sheaths densely scabrous; ligule 2–3.5 mm long ..... *P.tayacajaensis*
– Combination of characters not as above; spikelet proximal lemmas glabrous or sparingly pubescent on the keel, and sometimes marginal veins; distal lemmas often glabrous throughout; sheaths smooth to densely scabrous; ligule 1–10 mm long 27

27 (26). Lower culm sheaths usually puberulent in the throat margins and/or along the collar margins, surfaces smooth to lightly scabrous; upper culm leaf ligules 1–5(–7) mm long, abaxially puberulous or scabrous; lowest floret of spikelets hermaphroditic, upper florets commonly pistillate; spikelets 3.5–5 mm long; lower lemma 3.6–4 mm long, intermediate veins faint to moderately pronounced; palea keels usually finely scabrous to some degree; anthers mostly 0.6–1.5 mm long ..... *P.aequatoriensis*
– Lower culm sheaths glabrous in the throat margins, surfaces nearly smooth to densely scabrous; upper culm leaf ligules 4–10 mm long, abaxially smooth or faintly scabrous; all florets of spikelets hermaphroditic; spikelets 2.3–3.5(–4) mm long; lower lemma 2.3–3(–3.5) mm long, intermediate veins distinctly pronounced; palea keels usually muriculate, sometimes minutely scabrous; anthers 1.3–2.1 mm long. ..... *P.trivialis*

Chapter 7

Bartsia lydiae, a new species of *Bartsia* sect. Laxae (Orobanchaceae) from the southern Peruvian Andes with a revised key to *Bartsia* sect. Laxae

S.P. Sylvester

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Bartsia lydiae, a new species of *Bartsia* sect. Laxae (Orobanchaceae) from the southern Peruvian Andes with a revised key to *Bartsia* sect. Laxae

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Abstract

A new species of *Bartsia* sect. Laxae is described and illustrated from the Cordillera Vilcanota, southern Peru. The species is distinct from all other members of sect. Laxae in being covered with persistent glandular hairs and having a reddish purple corolla. The species is a common element of undisturbed puna vegetation in the Cordillera Vilcanota, being associated with *Polylepis* forests. A revised key to *Bartsia* sect. Laxae is included to accommodate this new species.

Introduction

The genus *Bartsia* Linnaeus (1753: 602) comprises 49 species, its centre of diversification being in the Andes of South America with 45 species endemic to this area (Molau 1990). Peru contains the largest diversity of *Bartsia* with 35 species (Brako & Zarucchi 1993, Ulloa et al. 2004) found scattered throughout the Andean foothills and mountain chain, 14 of which are endemic (León 2006). *Bartsia* sect. Laxae Molau (1990: 50) is a morphologically well-defined group currently containing 10 species which are distributed from Venezuela to Bolivia and Chile. The section is distinguished by a campanulate calyx with the lobes reflexed from mid anthesis and an exserted capitate stigma. The taxonomy of *Bartsia* is still in debate with recent phylogenetic studies (Scheunert et al. 2012) suggesting the transfer of all South American *Bartsia* species to the resurrected genus *Bellardia* All. (1785: 61). Scheunert et al. (2012) do clearly state, however, that this is perhaps premature as only 3 out of the, now, 46 Andean *Bartsia*'s have been sequenced to date including just one species from sect. Laxae.

Bartsia, in the past, was considered notoriously difficult due to the superficial similarities of herbarium specimens and the occurrence of many mixed herbarium collections which deterred most taxonomists from attempting to revise the genus. Despite these difficulties, Molau (1990) produced the first concise world revision of the genus, benefitting the taxonomy of *Bartsia* immensely and allowing the specimens collected to be easily recognised as a species new to science. Based on morphological studies of dry and living material in collections and field studies, I describe this new species of *Bartsia* sect. Laxae with a persistent glandular-pubescent indumentum and reddish purple corolla, morphologically distinct from all other species of sect. Laxae.

Taxonomy

Bartsia lydiae S.P.Sylvester, *sp. nov.* (Fig. 1–3)

Species perenne distincta ab aliis speciebus notis sect. Laxae, a quibus caulibus vel foliabus hirsutus, pilis glandulosis, corolla purpurea.

Type:—PERU. Cusco, Prov. Urubamba: Distr. Urubamba, Área de Conservación Privada (ACP) Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of laguna Ipsaycocha, forest on the SW side of laguna Manalloqsa, 4614m, S13° 11' 59.2" W72° 08' 39.9", 23 June 2012, *S.P. Sylvester 1754* (holotype USM!, isotypes CUZ!, GB!, ID!, MO!, Z!)

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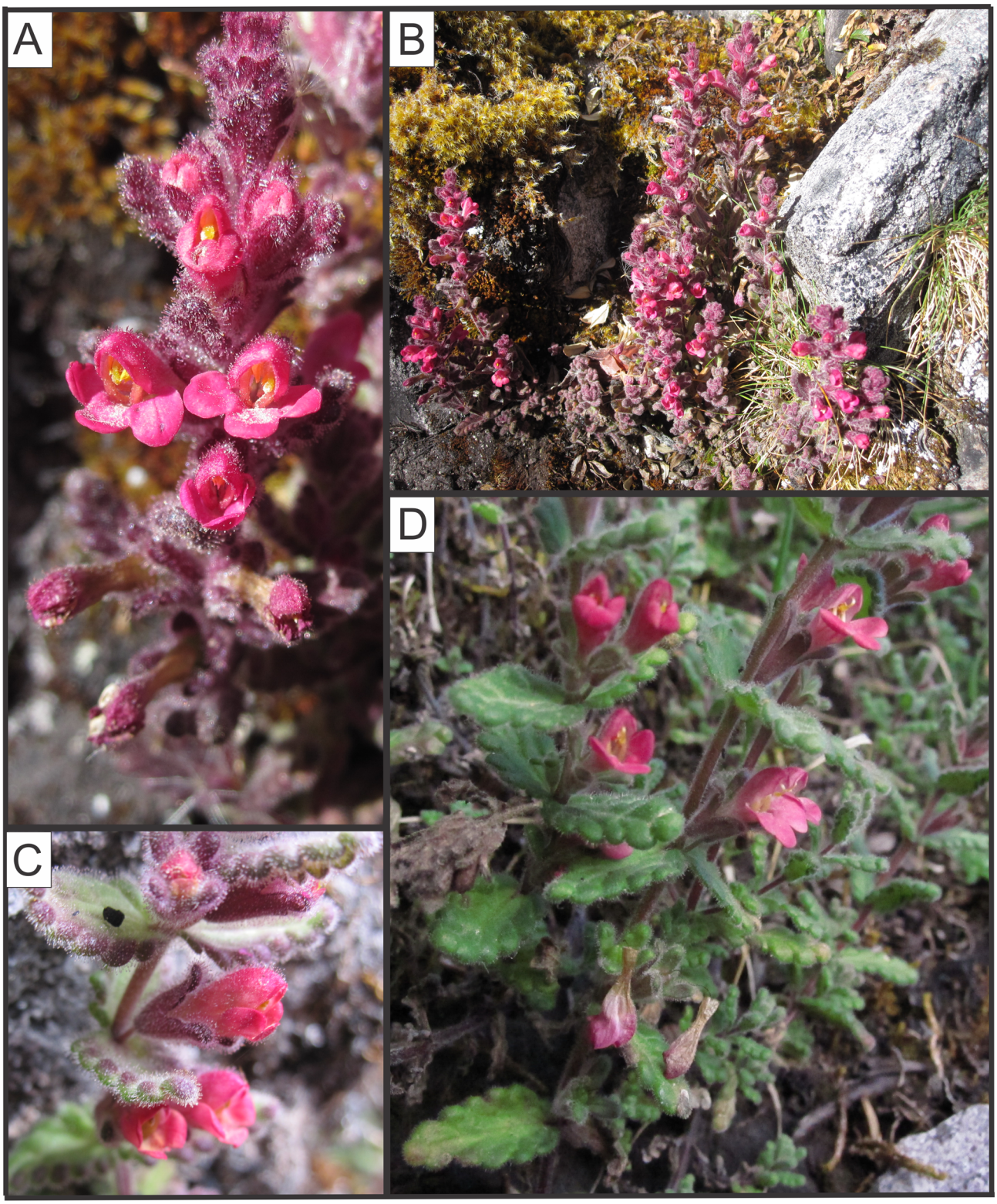

FIGURE 1. Features of *Bartsia lydiae*. **A.** Inflorescence of the type specimen, *S.P. Sylvester 1754*. **B.** Habit (type specimen, *S.P. Sylvester 1754*). **C.** Immature flowers with the corolla lip incurved or straight. The glandular indumentum on the bracts is easily noticeable, the deflexed calyx lobes are characteristic of sect. Laxae (*S.P. Sylvester 1407*). **D.** Mature flowers in the foreground showing the deflexed corolla lip (*S.P. Sylvester 1649*). Photographs taken by S.P. Sylvester.

Ascending perennial (rarely annual) herb, (0.1–)0.5–0.8 m tall, arising from a perennial woody crown, the shoots ascending or divaricate, branched chiefly at the base. Stems retrorsely white hirsute to villous with glandular hairs (the glands deciduous). Leaves divaricate, generally remote on stems, ovate to elliptic, 9–22(–28) × 4–8(–12) mm,

obtuse, rounded to truncate at base (sometimes cuneate in smaller leaves and semi-amplexicaul in larger leaves), green to purple (in areas exposed to sunlight), hirsute with white glandular hairs throughout, the margins deflexed to slightly revolute, evenly crenate with 4–6(–7) lobulae along each side. Inflorescence loose, 5–12 cm long, and comprising 4–9 floral nodes, the lowermost internode 0.6–1.5 cm in fruit; bracts similar to foliage leaves; pedicels 2–4(–6) mm long. Flowers ascending, 9–12(–15) mm long. Calyx campanulate, 7–9(–10.5) mm long at anthesis, dark green to purple, hirsute with glandular, multicellular hairs (the hairs white with dark glands) and glandular moniliform hairs towards the calyx lobe apex, ± equally cleft, the lobes subulate, reflexed, obtuse to subacute, entire, the clefts 40–60% of calyx length. Corolla glandular puberulous with moniliform hairs, the galea cucullate, reddish purple, 9–12(–15) mm long, equal to or shorter than the lip, sometimes longer than the lip (galea length 0.85–1.0(–1.2) × lip length), the lip varying from deflexed and spreading in mature flowers to incurved and appressed in young flowers, 10–14 × 5–8 mm, ± gibbose, reddish purple, the tube puberulous with glandular moniliform hairs, light reddish purple fading to white. Anthers included, yellow, sparsely villous, ± distinctly mucronate, (1.2–)1.4–1.9 mm long. Style 7–11 mm; stigma yellow-green to yellow, slightly bilobate. Capsule ovoid, 7–9 mm long, white setose, purplish. Seeds small, 0.6–0.8 mm long, pale brownish-white, relatively narrow winged.

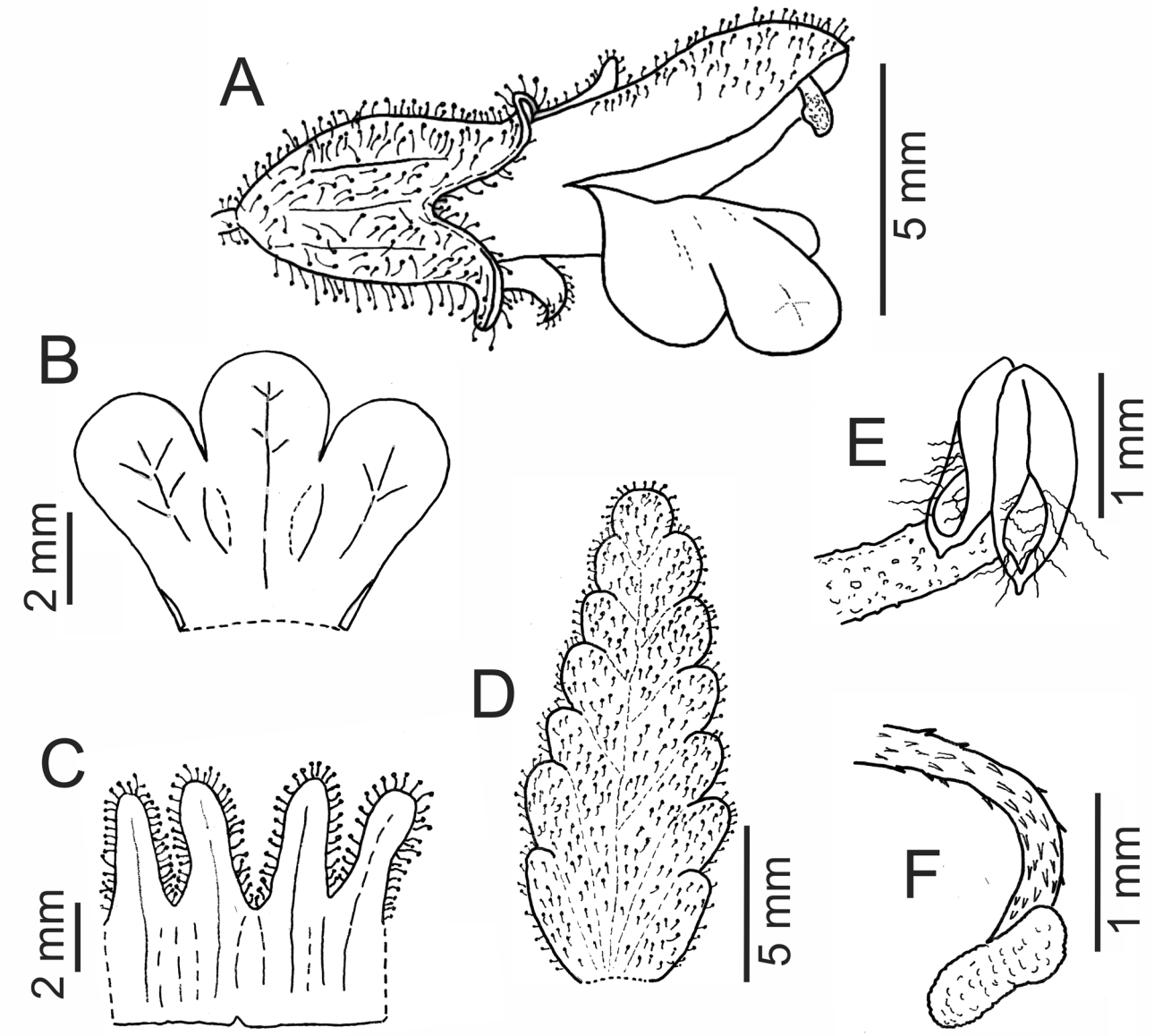

FIGURE 2. *Bartsia lydiae*. **A.** Flower. **B.** Corolla lip. **C.** Calyx, opened out from the ventral side. **D.** Bract, adaxial view. **E.** Anther. **F.** Style. Illustration based on type specimen *S.P. Sylvester 1754*.

Distribution:—(Fig. 3) Restricted to undisturbed areas of *Polylepis* Ruiz & Pav. (1794: 80) woodland in hard to access areas throughout the Cordillera Vilcanota, Cusco, Peru, at 4220-4820 m a.s.l.. Known from four localities; 1) Cliff ledges of the prominent SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán. 2) Ledges of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán. 3) Surroundings of Laguna Manalloqsa, ACP Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of Laguna Ipsaycocha. 4) Terrace on the N side of Laguna Qellococha, 5 km N of Huayocari village.

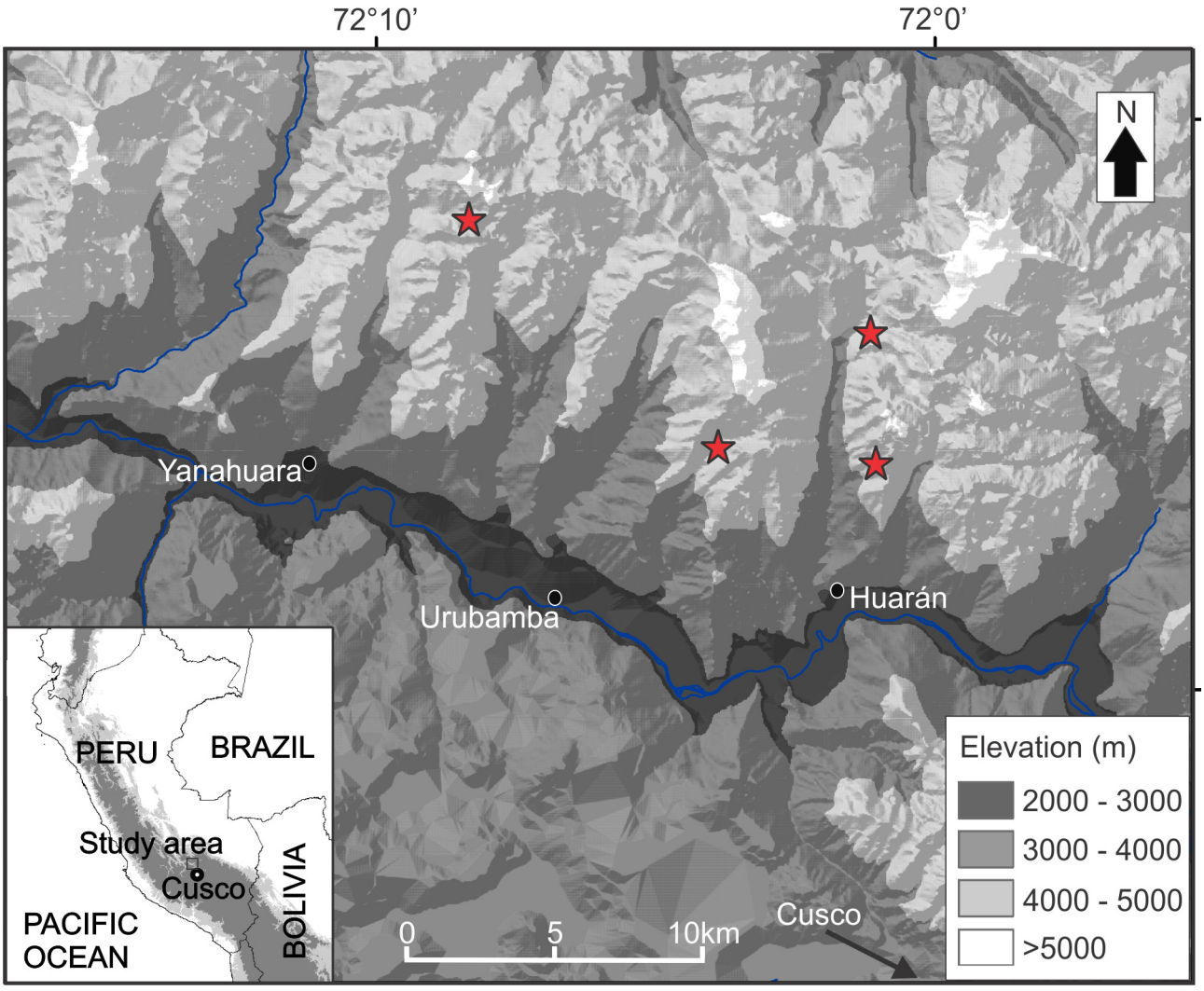

FIGURE 3. Distribution map of *Bartsia lydiae* with sites where the species was encountered marked with a star. ASTER DEM raster map provided by METI and NASA Land Processes Distributed Active Archive Center.

Habitat:—Relatively dry and exposed sites in montane *Polylepis* forest and forest edges, often sheltered close to rocks.

Etymology:—The name '*lydiae*' is in recognition of botanist Dr. Lydia Hantsch and her scientific accomplishments.

Additional specimens examined:—PERU. Cusco. Prov. Calca: Distr. Calca, large ledge situated on the prominent SW facing cliff face 1 km SE of Cancha Cancha village, Huarán, 4524 m, S13° 14' 35.1" W72° 01' 13.5", 15 October 2010, *S.P. Sylvester 127* (CUZ!, Z!); Distr. Calca, large ledge situated on the prominent SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4535 m, S13° 14' 35.3" W72° 01' 13.6", 24 March 2011, *S.P. Sylvester 878* (CUZ!, ID!, Z!); Distr. Calca, large ledge situated on the prominent SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4522 m, S13° 14' 35.2" W72° 01' 14.1", 21 March 2011, *S.P. Sylvester 815* (CUZ!, Z!); Distr. Calca, large ledge situated on the prominent cliff 1km S (150°) of Cancha

Cancha village, Huarán, 4504m, S13° 14' 35.6" W72° 01' 14.8", 27 March 2011, *S.P. Sylvester 939* (CUZ!, LPB, Z!); Distr. Calca, the Southern-most point of the prominent ledge situated on the SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4504 m, S13° 14' 36.6" W72° 01' 14.6", 07 April 2011, *S.P. Sylvester 1017* (CUZ!, Z!); Distr. Calca, at the far S of the prominent ledge situated on the SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4544 m, S13° 14' 36.3" W72° 01' 14.4", 07 April 2011, *S.P. Sylvester 1026* (CUZ!, Z!); Distr. Calca, the prominent ledge situated on the SW facing cliff face 1.5 km S (170°) of Cancha Cancha village, Huarán, 4544 m, S13° 14' 36.3" W72° 01' 14.4", 24 March 2012, *S.P. Sylvester 1407* (CUZ!, Z!); Distr. Calca, the *Polylepis* forest to the E of the prominent tower known by locals as "Kontorqayku", 5 km NE of Huarán, 4251 m, S13° 16' 09.6" W72° 01' 04.9", 06 June 2012, *S.P. Sylvester 1649* (CUZ!, GB!, ID!, Z!); Prov. Urubamba: Distr. Urubamba, ACP Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of Laguna Ipsaycocha, ledges on cliff side 250°W of Laguna Manalloqsa, 4624 m, S13° 11' 59.3" W72° 08' 39.7", 01 February 2011, *S.P. Sylvester 464* (Z!); Distr. Urubamba, ACP Mantanay, 10 km up the valley from Yanahuara in the small valley 3 km E of Laguna Ipsaycocha, topmost of the ridge to the W of Laguna Manalloqsa, 4819 m, S13° 12' 09.5" W72° 08' 44.3", 25 June 2012, *S.P. Sylvester 1730* (CUZ!, GB!, ID!, MO!, Z!); Distr. Huayllabamba, terrace situated on the N side of Laguna Qellococha and to the E of the waterfall, 5 km N of Huayocari village, 4221 m, S13° 16' 35.8" W72° 03' 01.4", 09 March 2011, *S.P. Sylvester 680* (CUZ!, Z!).

Discussion:—*Bartsia lydiae* is easily recognised in the field by its glandular indumentum covering the leaves, stems and flowers and the reddish purple flowers with deflexed corolla lip (in mature flowers) and reflexed calyx lobes. The whole plant is covered with a persistent glandular-haired indumentum that separates it from all members of sect. Laxae except *B. adenophylla* Molau (1990: 63), which is a strictly annual plant with an erect, solitary habit and pale yellow flowers with glabrous anthers. *Bartsia lydiae* also bears resemblances to *B. flava* Molau (1990: 60) in the deflexed, wide (>5 mm) corolla lip but *B. flava* is distinguished by a yellow corolla and absence of glandular hairs.

Bartsia lydiae was found to occupy all study sites in the Cordillera Vilcanota (Fig. 3) whilst studying differences in vegetation composition between anthropogenically disturbed puna grasslands and undisturbed zonal vegetation of crag ledges as part of a larger study attempting to reconstruct the potential natural vegetation (PNV, Zerbe 1998) of the puna (Sylvester et al. *unpubl. data*). From personal observation, this species constitutes an important part of the natural vegetation in this part of the high Andes and its frequency and abundance within relict patches of near natural vegetation gives cause to believe that this is an indicator species for the PNV, although analysis of the data will be needed to verify this claim (Sylvester et al., *unpubl. data*). *Bartsia lydiae* has not been found in accessible, disturbed or secondary, vegetation at similar or lower elevations in the Andes of the Cuzco region, despite a more thorough botanical exploration. This may relate to the species susceptibility to disturbance from grazing and burning (Sylvester, *pers. observation*).

Key to the species of sect. Laxae (taken and revised from Molau, 1990)

1. All leaves with glandular hairs, the glands persistent 2
- Mature foliage leaves with eglandular hairs only 3
2. Much branched, ascending perennial (rarely annual); leaf margins evenly crenate with 4–6(–7) lobulae along each side; corolla reddish-purple; anthers sparsely villous ..... *B. lydiae*
- Solitary, erect annual; leaf margins deeply bullato-crenate with 10-14 lobelets along each side; corolla pale yellow; anthers glabrous ..... *B. adenophylla*
3. Corolla pure yellow, the galea sometimes suffused with purple, the lip deflexed, usually gibbose, and 5–8 mm wide ..... *B. flava*
- Corolla basically red to purple, the lip erect, less than 5 mm wide; gibbae absent 4
4. Anthers completely glabrous 5
- Anthers sparsely pilose to villous with white hairs 7
5. Leaves ovate, acute; calyx lobes erect ..... *B. remota*
- Leaves elliptic or lanceolate, obtuse; calyx lobes with the tips ± reflexed 6
6. Upper bracts distinct from foliage leaves, linear to elliptic, the margins entire, at least in the proximal half; Ecuador and N Peru ..... *B. mutica*
- Bracts similar to foliage leaves, lanceolate to elliptic, the margins crenate throughout; Chile ..... *B. chilensis*
7. Leaves densely white-tormentose; calyx glandular villous; N Peru ..... *B.tomentosa*
- Leaves pilose to hispid; Calyx pilose or hirsute, the hairs glandular or eglandular; Venezuela to N Bolivia 8

8. Inflorescence dense, subspicate, the upper bracts prominent, lanceolate to subulate, acute or acuminate, entire or laciniate-dentate, strigose with mostly eglandular hairs ..... *B. bartsioides*
- Inflorescence loose, the bracts smaller than foliage leaves, crenate, dentate or entire, at least the upper ones glandular-hirsute 9
9. Corolla with the galea orange-red and the lip bright yellow, the galea 1.4–1.7 × the length of the lip ..... *B. camporum*
- Corolla purple to deep red throughout, lip sometimes yellow-green, but then the galea 1.8–2.4 × the length of the lip 10
10. Calyx 10–15 mm long, the lobes straight, never reflexed; corolla lip yellow-green ..... *B. weberbaueri*
- Calyx 6–15 mm long, when more than 10 mm long the corolla lip usually red; calyx lobes reflexed..... *B. inaequalis*

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Chapter 8

A new species of *Moranopteris* (Polypodiaceae) from inaccessible ledges in the high Andes of Peru

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A New Species of *Moranopteris* (Polypodiaceae) from Inaccessible Ledges in the High Andes of Peru.

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Abstract*—*Moranopteris inaccessa, here described and illustrated, is a new species from southern Peru. Plants were collected in the Abra Málaga private conservation area from steep ledges accessible only with mountaineering equipment. *Moranopteris inaccessa* differs from its congeners by the combination of elongate membranaceous laminae that are 1-pinnate-pinnatifid. Found at 4,427 m, its distribution is over 500 m higher in elevation than any other species of *Moranopteris*. Phylogenetic analyses of *atpß*, *rbcL*, and *trnL-trnF* molecular sequences, using maximum parsimony, maximum likelihood, and Bayesian analysis support *M. inaccessa* as sister to *M. longisetosa*. The two are similar in their elongate and highly divided leaves compared to other species of *Moranopteris*. The discovery of this new species highlights the value of undertaking botanical surveys of undisturbed vegetation patches in the high Andes that potentially host unrecognized plant diversity.

Keywords—fern; grammitid, phylogenetics; puna; taxonomy

High elevation Puna grasslands, found above 3,900 m in the central Andes, have undergone dramatic alteration over the past several millennia as a result of large-scale human land use (Thompson et al. 1988; Burger 1992; Burns 1994; Chepstow-Lusty et al. 1996; Chepstow-Lusty and Winfield 2000; Moraes et al. 2006; Kuentz et al. 2011). Consistent burning and grazing has resulted in a vegetation formed almost exclusively of plants adapted to these anthropogenic pressures (Laegaard 1992; Becerra 2006), with susceptible species being restricted to areas inaccessible to grazing animals and the spread of human-induced ground fires, such as steep cliffs and ledges. The vegetation of these inaccessible areas, some of which can be reached using mountaineering equipment, can be seen as a proxy for the potential natural vegetation of the Puna provided that the vegetation is zonal and not strongly influenced by the surrounding rock faces (Sylvester et al. 2014a). Recent surveys of this potential natural Puna vegetation found on inaccessible ledges in the Cusco region, southern Peru, have yielded a number of plant species new to science (Sylvester 2014; Sylvester et al. 2014a, unpubl. data), including an undescribed grammitid fern that we recognize here, in the genus *Moranopteris* R. Y. Hirai & J. Prado.

Polypodiaceae have undergone massive generic re-circumscription following the results of molecular phylogenetic analyses (Ranker et al. 2004; Sundue et al. 2010). Neotropical grammitid genera have been found to form a grade, with a large tropical Asian clade comprising over 500

species (Sundue et al. 2014). The genus *Moranopteris* was recently described in order to include the Neotropical species of *Micropolypodium* Hayata sensu Smith (1992) and members of Smith's (1993) *Terpsichore* A. R. Sm. group 5, the *T. achilleifolia* group (Hirai et al. 2011). Hirai and Prado (2012) recognized 28 species of *Moranopteris* with *Micropolypodium* now being restricted to three Asian species whilst *Terpsichore* is restricted to ca. 12 Neotropical species (M. Sundue, unpubl.). *Moranopteris* is sister to that clade, and the estimated split of these two lineages is estimated to have occurred 24 ma (26–23 ma), with the crown group age of *Moranopteris* estimated to be 13.8 ma (19.8–9.5). Diagnostic characters of *Moranopteris*, namely rhizome scales with golden-brown translucent and turgid cells, branched hairs with glanduliform cells, and reddish setae, helped to identify the plant from Abra Málaga as a member of *Moranopteris* R. Y. Hirai & J. Prado.

The Abra Málaga plant is unusual in that it differs from most other *Moranopteris* by its epipetric habit and by having elongate 1-pinnate-pinnatifid membranaceous laminae. Most *Moranopteris* are epiphytic and are characterized by having short, pinnatisect herbaceous laminae (Hirai and Prado 2012). The Abra Málaga plant also differs from most other *Moranopteris* by having pinnate veins. Most species of *Moranopteris* have 1-furcate veins, and a small number have simple veins. Other grammitid genera most commonly have pinnae with simple veins if they are relatively small plants, or pinnate veins if they are relatively large plants (Sundue 2010). Thus, we raise the question whether the pinnate veins in the Abra Málaga plant could be a plesiomorphic character for the genus. To better understand the relevance of these characters, we conducted a phylogenetic analysis to determine the systematic relationships of the Abra Málaga plant to other species of *Moranopteris*.

MATERIALS AND METHODS

***Molecular Phylogenetic Analyses*—**The systematic position of the Abra Málaga plant was determined by comparison with 22 other species of *Moranopteris*. Most of these sequences were generated by Hirai et al. (2011) and the dataset used here is similar. It differs by the inclusion of the new species and *M. sherringii* (Baker) R. Y. Hirai and J. Prado. The outgroup taxa include *Micropolypodium* and a selection of species from across the grammitid phylogeny. We PCR-amplified three plastid DNA markers from the holotype: the *atpß* and *rbcL* coding regions, and the *trnL-trnF* intergenic spacer. DNA extraction and PCR amplification protocols followed those of Labiak et al. (2010). DNA sequencing was performed at the Greenwood Molecular Biology Facility at the University of Hawai‘i at Mānoa. Sequences generated as part of this study were submitted to GenBank. Accession numbers and vouchers for all sequences used in our analyses are provided in the appendix.

Sequences were edited and contigs were produced using Geneious 6.17 (Biomatters Ltd., San Francisco, California) and the MAAFT plug-in was used to produce alignments. For each aligned marker, optimal data partitioning and models of substitution evolution were estimated using AICc in partition finder (Lanfear et al. 2012). The resulting best scheme included four partitions, with separate HKY + I + G partitions for the first and second position nucleotide for both *atpß* and *rbcL*, a HKY partition for the third position nucleotide of *atpß* and *rbcL*, and a GTR + G model for the *trnL-trnF* intergenic spacer. These were implemented in the Bayesian and likelihood tree searches. We conducted tree searches using maximum parsimony (MP), maximum likelihood (ML) and Bayesian (MB) analyses. Maximum parsimony tree searches

were performed using TNT (Goloboff et al. 2008) employing a New Tech search strategy set at level 15 implementing tree fusing, sectorial search, and the parsimony ratchet. Maximum likelihood tree searches were conducted using RAxML (Stamatakis 2006) through the CIPRES portal (Miller et al., 2010) with independent searches for the 'best tree' and with 1,000 bootstrap replicates. Bayesian tree searches were conducted using MrBayes (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). We conducted independent runs for 10 million generations. Each run included four chains (one cold, three heated) with unlinked parameters, chain temperature set to 0.2, and uniform priors. The posterior was sampled every 1,000 generations, and the first 25% discarded as "burn-in". Convergence was estimated by inspection of the parameters in TRACER v 1.5 (Rambaut et al. 2013).

TAXONOMIC TREATMENT

Moranopteris inaccessa Sundue & S. P. Sylvester sp. nov. — TYPE: PERU. Cusco, Provincia Urubamba, Distrito Ollantaytambo, Abra Málaga, in the middle of the south facing cliff found 1.5 km SW of the Abra Málaga church, 4,427 m, 13°08'43.9"S, 72°18'26.7"W, 25 May 2012, *S. P. Sylvester 1628* (holotype: VT!; isotypes: CUZ!, LPB!, UC!, Z!).

Diagnosis— Differs from *Moranopteris longisetosa* by smaller pinnae (3–7 × 1.5–3 mm) that are shallowly pinnatifid with a single lobe instead of being deeply and regularly lobed.
Plants epipetric; rhizomes 0.8–1.4 mm wide, short-creeping, radially symmetrical, with radial root insertion and spiral phyllotaxis, scaly, rhizome scales 0.5–1.6 × 0.2–0.5mm, ovate to oblong, golden-brown, translucent, the cells semi-turgid, base weakly cordate, the apex rounded to acute, the margin sparsely provided with glanduliform projections; leaves pendent, 10–20 × 0.8–1.5 cm; petiole 5–8 cm long, 0.2–0.3 mm wide, blackish; laminae 8–13 × 0.6–1.5 cm, narrowly oblanceolate, 1-pinnate nearly throughout, with (25–)30–50 pinnae, the apex pinnatisect, medial pinnae 3–7 × 1.5–3 mm, oblong, the base adnate and decurrent basiscopically, the apex rounded, the acroscopic margins a single shallow lobe, otherwise the margins entire, the proximal 10–14 pinnae reduced, with 4–6 pinnae 1/3 to 1/2 the length of medial pinnae, and the 5–12 basal-most pinnae reduced to minute protuberances 0.1–0.2 mm long; rachises and both sides of the lamina surfaces moderately to densely covered with setae and hairs, the setae up to 2.5 mm long, reddish, terete, spreading, the hairs up to 0.5 mm long, whitish or hyaline, simple or 1–3-branched, the branches terminating in glanduliform cells; lamina tissue membranaceous, light green; veins pinnate, terminating in hydathodes adaxially, the hydathodes whitish, non-cretaceous; sori round, 5–6 per pinna; spores trilete, globose, green. Figures 1–2.

Additional Specimens Examined— PERU. Cusco, Província Urubamba, Distrito Ollantaytambo, Abra Málaga, a gully found on the south facing cliff 1.5 km SW of the Abra Málaga church, 4,429 m, 13°08'43.8"S, 72°18'26.6"W, 14 November 2010, *S. P. Sylvester 300* (Z).

Ecology and Distribution—Plants forming dense colonies among bryophytes, Cyperaceae and Poaceae on sheltered rock ledges, ca. 4,430 m (Fig. 2). Known only from the two collections made at Abra Málaga. This private conservation area is at a confluence between the humid Cordillera Vilcabamba and the dry Cordillera Urubamba and receives updrafts of moist air from

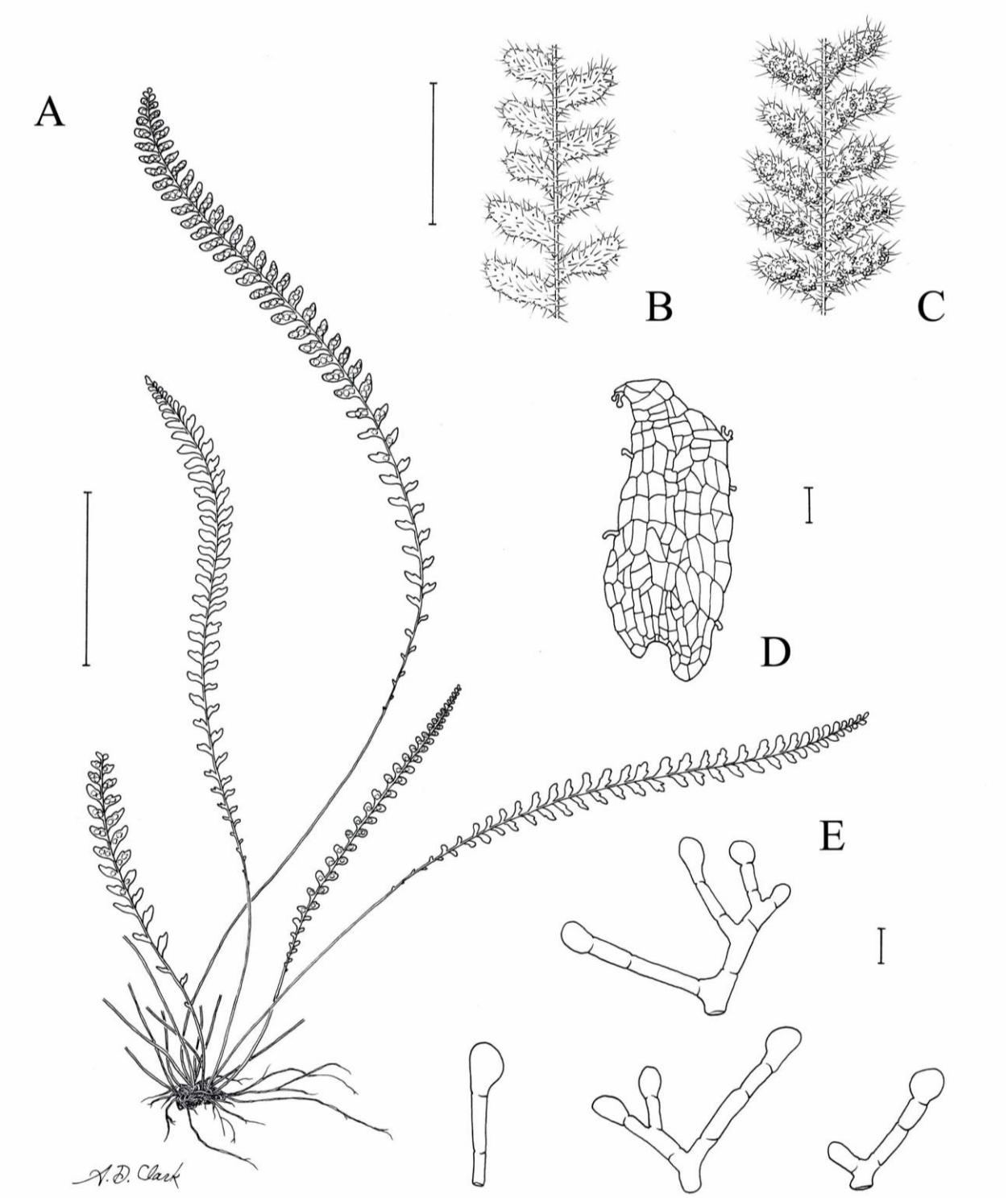

FIG. 1. *Moranopteris inaccessa*. A. Habit, scale bar = 5 cm, B. Detail adaxial lamina, scale bar = 1 cm, C. Detail abaxial lamina, scale bar = 1 cm, D. Rhizome scale, scale bar = 1 mm, E. Branched hairs, scale bar = 0.1 mm.

the Amazon basin creating a humid climate (see Sylvester et al. 2014a for details on the climate). It is the only stand of conserved *Polylepis* Ruiz & Pav. woodland in the Cusco region where intentional burning and firewood harvest is prohibited. It has been fenced-off to livestock since 2001 (Ecoan-Peru 2010). The site includes floristic elements of both the humid páramo and dry Puna vegetation.

Grammitids are primarily found growing at upper elevations (Kessler et al. 2001), and include the highest recorded elevation for a vascular epiphyte (4,542 m, *Melpomene peruviana* (Desv.) A. R. Sm. & R. C. Moran) (Sylvester et al. 2014b). At 4,427 m, *Moranopteris inaccessa* ranks among the highest-dwelling grammitids in the Andes. It is over 500 m higher in elevation than the highest recorded locality for any species of *Moranopteris* (*M. longisetosa* (Hook.) R. Y. Hirai & J. Prado, 3,850 m; Hirai and Prado 2012).

The rarity of *M. inaccessa* is difficult to determine. It may, in fact, be widespread on other difficult to access ledges, but this remains to be determined as no other similar sites were studied close to the Abra Málaga reserve. Other sites studied were located at least 19 km east or 60 km west and experience different climatic conditions from the present site (Sylvester et al. unpubl. data). This species was not found to occur in the grazed, burnt vegetation surrounding the ledge site and this may reflect the species susceptibility to disturbance from grazing and/or burning (Sylvester, pers. observation).

Comments*—Moranopteris inaccessa* is distinguished by its epipetric habit and its narrow, elongate 1-pinnate leaves with membranaceous laminae and pinnate veins. Pinnate veins are uncommon in *Moranopteris*, and are otherwise only known from *M. achilleifolia*, *M. gradata* (Baker) R. Y. Hirai & J. Prado, and *M. longisetosa* (Hook.) R. Y. Hirai & J. Prado. Each of these can be distinguished from *M. inaccessa* by laminar dissection and/or rhizome scales. *Moranopteris gradata* and *M. achilleifolia* both differ by having scales with non-glandular margins. *Moranopteris grada* further differs by having entire pinnae. *Moranopteris achilleifolia* and *M. longisetosa* both differ by having pinnae with several acute lobes along both sides of the pinna and by having chartaceous laminae.

The membranaceous laminae of *Moranopteris inaccessa* are reminiscent of leaves in *Alansmia* M. Kessler et al. and *Galactodenia* Sundue & Labiak. However, phylogenetic analyses of cpDNA sequences (Ranker et al. 2004; Sundue et al. 2010) do not support a close relationship for either of these genera to *Moranopteris*; thus their similarity is interpreted as an example of the convergent morphological patterns that occur frequently among grammitid ferns (Ranker et al., 2004). *Alansmia* can be distinguished from *Moranopteris* by having stellate or clustered setae on the petioles and laminae (at least in most species), and by its frequently ciliate sporangia (Kessler et al. 2011). *Galactodenia* can be distinguished by its unique glandular hairs. *Moranopteris* and *Galactodenia* both have branched glandular hairs, but those of *Galactodenia* differ by having clavate glandular cells that are hyaline, milky-white to gray or golden brown. Those of *Moranopteris* are spherical and clear (Sundue et al. 2012).

Although we are loathe to describe a new species based on only two collections from a single site, in this case, this seems to be the best course of action. It is unlikely that additional collections will be made soon and, by describing it, we draw attention to the importance of inaccessible ledges as refuges for an unrecognized signature of plant diversity in the Puna landscape. Furthermore, each duplicate of the type collection includes ample material with multiple plants represented. Thus, there does not seem to be a risk that the type represents a morphologically aberrant plant. Hirai (pers. com.) suggested that these collections might

FIG. 2. A–D, Abra Malagá. A. the type locality. B. Detail of habitat. C. Botanizing the ledges. D–E. *Moranopteris inaccessa* from the type locality. D. Adaxial leaf surface. E. Habit.

represent a hybrid plant between *M. longisetosa* and some other species of *Moranopteris* or even another grammitid genus. The two species do share some characters in common, but we interpret these as the result of shared evolutionary history, not hybrid origin. Molecular sequences of all three chloroplast regions sequenced from *M. inacessa* show distinct SNPs not found in *M. longisetosa*. Spores of *M. inaccessa* are well formed, suggesting that it is a sexually reproducing plant. Furthermore, the morphology of *M. inaccessa* does not appear to be intermediate between *M. longisetosa* and some other congener, and there are no characters that would suggest hybridization between different grammitid genera.

***Etymology*—** Derived from the Latin word inaccessus (= inaccessible) in reference to the nearly inaccessible ledges from which it is known.

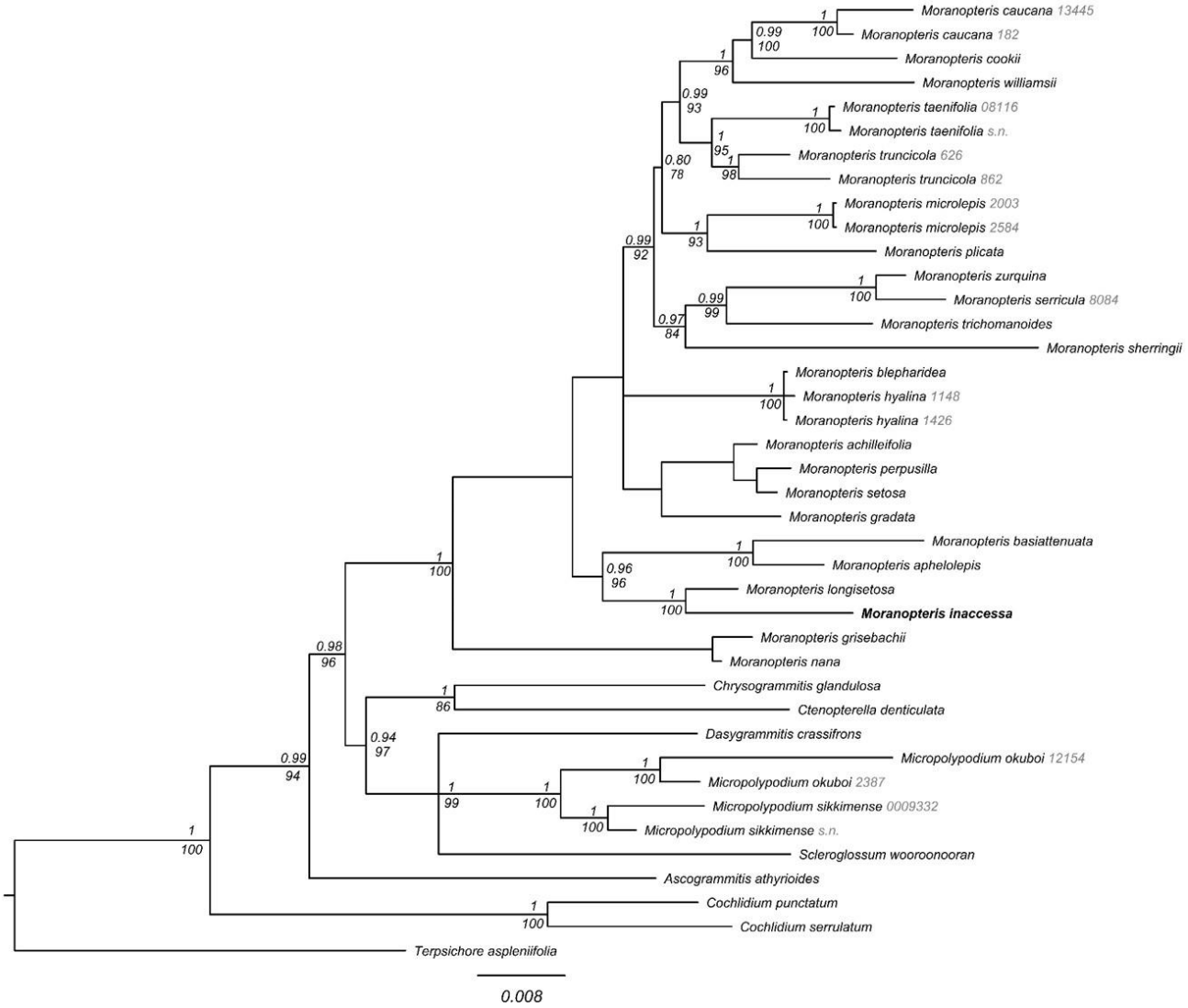

FIG. 3. Consensus tree resulting from the Bayesian analysis. Numbers above nodes are Bayesian posterior probabilities. Numbers below nodes are maximum likelihood bootstrap values. Numbers following binomials are collection numbers. Scale bar represents substitutions per site inferred from the Bayesian analysis.

***Phylogenetic Analysis*—** Analysis of cpDNA (Fig. 3) resolved *Moranopteris* as monophyletic with a posterior probability (PP) of 1, and 100% Maximum Likelihood Bootstrap with *Moranopteris inaccessa* recovered in one of the early-diverging lineages (1 PP, 100% ML). Overall topologies under ML and Bayesian inference were similar to that of Hirai et al. (2011), including several weakly supported backbone nodes. One exception was the position of *M. nana*. Relationships of this species were not well supported in any analyses. In our Bayesian analyses, it was resolved sister to *M. grisebachii* in a clade sister to the remainder of the genus. In our likelihood analyses it was deeply nested within the genus, sister to *M. purpusilla* (not shown). Parsimony analysis found both of these results among the most parsimonious trees. Consequently, in a strict consensus, these taxa, along with *M. setosa* and *M. achilleifolia*, collapsed into a polytomy with the remainder of *Moranopteris* (not shown). Under all analyses, the West Indies endemic, *Moranopteris sherringii* (Baker) R. Y. Hirai, which has not previously been included in any analyses, was resolved as sister to a clade of small-leaved species whose distributions include the West Indies, Central America, and the Andes.

Phylogenetic Relations of Moranopteris inaccessa — *Moranopteris inaccessa* was resolved as sister to *M. longisetosa* (Hook.) R. Y. Hirai & J. Prado in all analyses (1 pp, 100% ML BS). Morphological characters supporting this relationship include 1-pinnate laminae, pinnate veins, and rhizome scale margins with glanduliform cells. The two species are also similar in having large, elongate leaves relative to other *Moranopteris* spp., and in inhabiting high elevation sites in the Andes. The two can be readily distinguished by differences in lamina cutting and pinna length. *Moranopteris longisetosa* has 6–70 × 2.0–7.5 mm pinnae that are deeply pinnatifid with usually 5–8 acute lobes per pinna that are cut nearly to the costa (Hirai & Prado, 2012).

***Venation in Moranopteris* —** Most species of *Moranopteris* have 1-furcate veins and our phylogenetic results suggest that this is the plesiomorphic state for the genus. Our outgroups are composed of taxa with either simple or pinnate veins. In our results, simple veins evolve once within *Moranopteris*, in the clade comprising *M. caucana*, *M. cookii*, and *M. wilsonii*. Pinnate veins appear twice: once in the sister group of *M. inaccessa* and *M. longisetosa*, and once in *M. gradata*. Thus, we do not find any evidence that pinnate veins are plesiomorphic in *Moranopteris*. Instead, they appear to be derived.

Discussion — With the addition of this new species, *Moranopteris* now comprises 29 species, nine of which occur in Peru. The Andean region contains the highest diversity of *Moranopteris* species (Hirai and Prado 2011) with 15 species now known to occur there. The discovery of this new species highlights the value of undertaking botanical surveys of undisturbed vegetation patches in the high Andes that potentially host unrecognized plant diversity.

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Chapter 9

Gentianella viridiflora (Gentianaceae), a new green-flowered *Gentianella* species from the Peruvian Andes

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Gentianella viridiflora (Gentianaceae), a new green-flowered *Gentianella* species from the Peruvian Andes

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Abstract
Gentianella viridiflora, a new species of *Gentianella* (Gentianaceae, Gentianeae, Swertiinae) from the Cordillera Vilcabamba, southern Peru, is described. Its yellowish-green corolla distinguishes it from other South American *Gentianella* species that share a similar set of morphological features. The new species is known only from the type locality and grows in grazed areas adjoining *Polylepis* woodland.

Resumen
Se describe *Gentianella viridiflora*, una nueva especie de *Gentianella* (Gentianaceae, Gentianeae, Swertiinae) de la Cordillera Vilcabamba, del sur del Perú. Se distingue de otras especies Sudamericanas de *Gentianella* morfológicamente similares, por el color amarillento-verde de la corola. La nueva especie es conocida solamente de la localidad típica y crece en áreas pastoreadas aledañas a bosquetes de *Polylepis*.

Key words
Central Andes, cleistogamy, grazing adapted, puna grassland

Introduction

In its current generic circumscription, *Gentianella* comprises ca. 250, mostly alpine, species which are distributed worldwide, with the exception of central and southern Africa (Struwe et al. 2002). The center of species diversity is found in the tropical Andes of South America, where the genus underwent a recent radiation (von Hagen & Kadereit 2001) with new species still being discovered (e.g., Pringle 2011, 2012a, 2014, Pringle & Grant 2012).

Taxonomically, it is difficult to get a grip on South American *Gentianella*. Insufficient sampling of high Andean areas, where the majority of species are found, and political instability of many regions on the continent, has confounded the study of this diverse genus. This, coupled with the often high degree of intraspecific morphological variability, may explain why there is no modern treatment even almost 100 years after the last complete monograph of South American *Gentianella* (Gilg 1916, then still placed as a subgenus within *Gentiana*). For Peru, Macbride (1959) provided an English translation of Gilg's (1916) species descriptions, together with comments and a preliminary key. He listed 97 species known from Peru, including a few newly described species (Reimers 1929, Briquet 1931). Brako & Zarucchi (1993) then published a checklist of the Peruvian species, including further new species (Fabris 1955, 1958, Pringle 1986) and reducing others to synonomy, bringing the total of Peruvian *Gentianella* species down to 82. Since then, several taxonomic studies (Pringle 2008, 2011, 2012a, 2012b, 2014, Pringle & Grant 2012) raised the number of species of *Gentianella* currently known from Peru to 95, with many being assigned IUCN conservation categories by Castillo et al. (2012).

The new species, *Gentianella viridiflora*, was found during recent botanical exploration in remote areas of the Cordillera Vilcabamba, southern Peru, for an ecological study assessing the impact of anthropogenic disturbance on natural vegetation and soils of the high-elevation puna grasslands of southern Peru (Heitkamp *et al.* 2014, Sylvester *et al.* 2014). In this study, disturbed accessible vegetation, which has been grazed and burnt consistently over millennia (Thompson et al. 1988, Chepstow-Lusty *et al.* 1996, 2009, Kuentz *et al.* 2011) was compared with pristine zonal

vegetation. *Gentianella viridiflora* was found to be a common element of disturbed puna woodland at one site which, due to its remoteness and long-term terrorist presence, can be considered very difficult to access and which may explain why this species has not been discovered until now.

Here, we describe and illustrate *Gentianella viridiflora* from the Cordillera Vilcabamba, Cusco region, Peru, and provide information about its habitat at the type locality.

Taxonomy

Gentianella viridiflora S. Pfanzelt & S.P. Sylvester, *spec. nov.* (Fig. 1, 2 A–B)

Type:—PERU. Cusco: Provincia La Convención, Distrito Vilcabamba, forest towards the top of the Totora-Purkay valley on the North side of the river, 3 km East of the Totora-Purkay village, 4171 m, 13°10'50.2"S, 73°03'33.0"W, 7 May 2013, *S.P. Sylvester 1951* (holotype USM!; isotypes LPB!, OLD!, Z!).

Differs from similar Andean Gentianella *species, with several decumbent to ascendent one-flowered stems, by its distinct yellowish-green, probably cleistogamous, flowers.*

Description:—Herbaceous, tap-rooted, probably annual or short-lived perennial of up to 14.5 cm height. Several stems from the base, there of 1.0–2.0 mm diameter, branched from the lower to mid-height stem nodes, ascendent; distal internodes slightly terete; basalmost internodes up to 21 mm, the upper ones generally twice as long as the subtending leaves. Leaves not connate at base; basal leaves spatulate, 18.5–27.1 × 4.8–6.6 mm, apices rounded; stem leaves spatulate to obovate-oblong, becoming smaller distally, 6.5–12.7 × 1.5–4.3 mm, apices rounded. Flowers solitary, erect, pentamerous, hermaphroditic, on long peduncles of up to 5.8 cm. Total length of calyx 7.3–9.0(–9.8) mm, calyx tube infundibuliform; calyx lobes oblong with slight constrictions just below the middle, slightly spreading (in the field), 3.3–4.8 × 1.3–2.2 mm (width at base), (0.95–)1.1–1.2 times as long as the tube, apices acute; no colleters on the adaxial side of the calyx base. Corolla yellowish-green, its lobes sometimes abaxially suffused with reddish purple at the tip and along the outer edge; corolla of terminal flowers 15.5–16.5 mm long, that of flowers of axillary branches on average smaller, 8.9–16.2 mm; corolla lobes ovate, (4.2–)7.1–9.0 × 3.7–4.5 mm, (0.4–)0.8–1.0(–1.2) times as long as the tube, apices acute. Sparse trichomes present at the site of filament insertion and distally towards the corolla lobe sinus, but sometimes absent. Filaments 2.1–3.6 mm long, inserted at about 0.7–0.9 times the height of the corolla tube. Anthers bluish, 1.3–2.2 mm long. Ovary cylindrical, 10.4–12.9 × 1.8–2.4 mm, subsessile to stipitate upon a gynophore up to 1.1 mm long; without conspicuous style; two stigmatic lobes, 0.6 × 0.7 mm. One U-shaped nectary at the base of each petal. Capsule 15.1–18.7 × 2.5–2.8 mm. Seeds dark brown, subglobose, foveate, 0.6–0.8 mm in diameter.

Distribution and habitat:—*Gentianella viridiflora* is known only from the type locality, the Totora-Purkay valley, where it was found to be locally abundant on heavily grazed mountain slopes on the edge of dense *Polylepis pepei* B.B. Simpson woodland or intermixed in more open grazed woodland from 4100–4200 m a.s.l. (Fig. 2 C-D). Up to 40 individual plants were encountered in a single 2×2-m^2 plot studied at the type locality. Indicator species analyses have retrieved this species as a significant indicator species of disturbed puna woodland in that area (Sylvester et al. *unpubl. data*). It is likely that heavy grazing maintains the niche of this species as it was not observed in areas with reduced grazing, probably because of out-competition for light by tussock grasses. The plants were found associated with other low-growing forbs such as *Azorella multifida* (Ruiz & Pav.) Pers., *Belloa kunthiana* (DC.) Anderb. & S.E.Freire, *Agrostis breviculmis* Hitchc., *Carex ecuadorica* Kük., and *Lachemilla pinnata* (Ruiz & Pav.) Rothm (Fig. 2). Despite thorough revision of specimens at CUZ, no other specimens of *G. viridiflora* have been found. However, the difficult access to valleys in the Cordillera Vilcabamba has probably led to this

province being under-sampled.

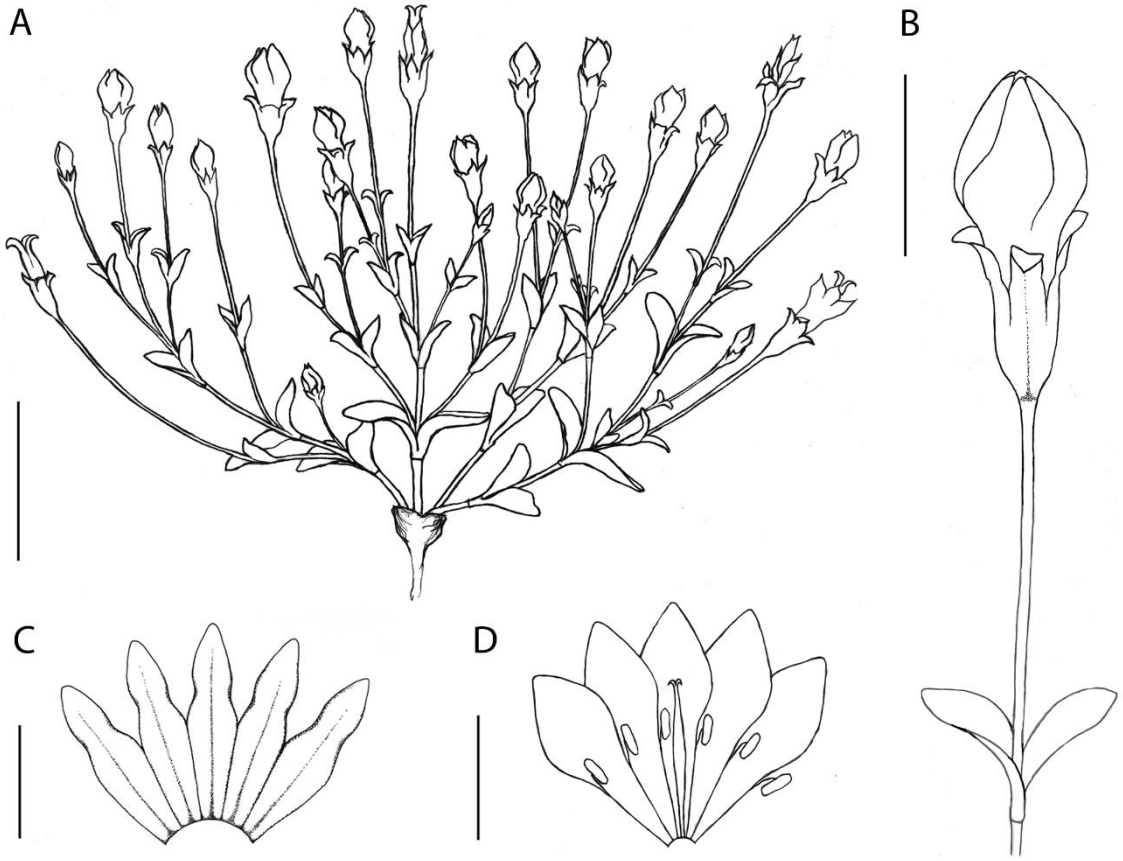

FIGURE 1. *Gentianella viridiflora*. A. Habit; B. Close up of a single one-flowered stem; C. Calyx spread out; D. Corolla spread out, showing the stamens and pistil in proportion to the corolla. Measurement bars A = 5 cm, B = 1 cm, C = 0.5 cm, D= 1 cm. Drawings by L. Ammann, based on the holotype (*S.P. Sylvester 1951).*

Comparison with similar species:—The yellowish-green corolla colour of *Gentianella viridiflora* is very similar to that of the Peruvian species *G. chlorantha* J.S.Pringle, *G. thyrsoidea* (Hook.) Fabris, and *G. weigendii* J.S.Pringle, and of the Bolivian species *G. macrorrhiza* (Gilg) Fabris ex T.N.Ho & S.W.Liu. *Gentianella chlorantha* from Amazonas is a subshrub with densely spaced leaves and subsessile flowers. *Gentianella thyrsoidea* from central Peru and *G. weigendii* from Ancash both feature a single primary stem and linear leaves. Their inflorescence is a many-flowered thyrse. *Gentianella macrorrhiza* from Cochabamba (Bolivia) has a thick rhizome covered with old leaf remains, lanceolate, glossy leaves, and globose corollas.

Among those Peruvian *Gentianella* species with yellow to yellow-red corollas that share a similar habit with *Gentianella viridiflora, G. tovariana* Fabris from Huancavelica differs in being a scapose perennial with red-tipped yellow flowers. Its corolla is glabrous within and the filaments are inserted in the lower third of the corolla tube. *Gentianella chrysosphaera* (Gilg) Zarucchi from Junin is a perennial with a stout caudex and a well-developed basal leaf rosette. The inflorescence is a 2-4-flowered cyme. The ovate calyx lobes have apiculate apices and the corolla is glabrous within. *Gentianella chrysotaenia* (Gilg) Zarucchi from central Peru has an inflorescence consisting of apical 3-flowered cymes. Additionally, several secondary one-flowered stems rise from the upper leaf axils. The corolla lobes are at least twice as long as the tube. Also, in the stout-rooted perennial *Gentianella incurva* (Hook.) Fabris from central Peru, the corolla lobes exceed the corolla tube. *Gentianella brunneotincta* (Gilg) J.S.Pringle, from north-central Peru, has subacute to acute rosulate leaves. First, flowers are yellow, later, they are tipped brownish. The corolla is glabrous

within.

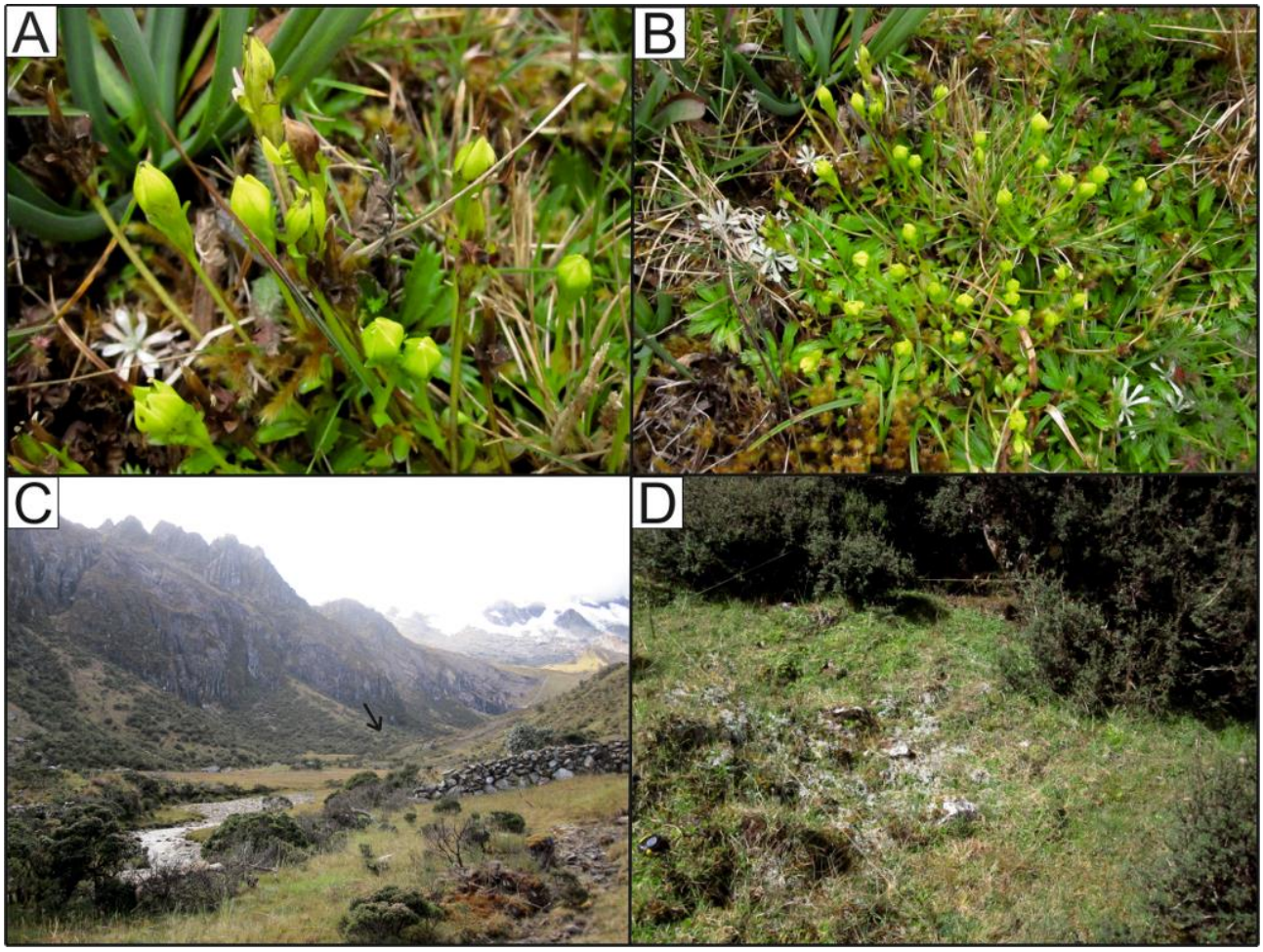

FIGURE 2. Gentianella viridiflora and habitat. A. Close up of the flowers of the holotype specimen (S.P. Sylvester 1951), showing the enclosed, possibly cleistogamous, green flowers; B. Habit of the holotype specimen; C. Type locality, specimens were found on the edges of the Polylepis woodland seen in the foreground and demarcated by an arrow; D. Habitat. Photographs taken by S.P. Sylvester.

Among the white, violet to blue-flowered species from central to south-central Peru that share a similar habit with Gentianella *viridiflora*, *Gentianella smithii* J.S.Pringle, a caespitose perennial from Ancash, differs in its connate leaf bases and in corolla lobes that are at least twice as long as the corolla tube, that does not bear any trichomes within. *Gentianella persquarrosa* (Reimers) J.S.Pringle from Cusco is very similar to *G. viridiflora* in habit, but it differs in corolla colour and its corolla lobes are twice as long as the corolla tube. This latter species and *G. potamophila* (Gilg) Zarucchi have obovate, rounded corolla lobes. *Gentianella vargasii* Fabris, whose type is also from Cusco, has basally connate leaves. Both calyx lobes and corolla lobes exceed the respective tubes by ca. twice its length. *Gentianella dolichopoda* (Gilg) J.S.Pringle from south-central Peru has basal leaves with a long, pseudopetiolate proximal portion and obovate corolla lobes that are much longer than the corolla tube. *Gentianella petrophila* (Gilg) Zarucchi from Junin has subacute to acute leaves, lanceolate calyx lobes and obovate corolla lobes that are much longer than the glabrous corolla tube. *Gentianella cerrateae* Fabris from north-central Peru is of rather small stature, with obovate, rounded corolla lobes. Also here, trichomes are absent. *Gentianella roseolilacina* (Gilg) J.S.Pringle from Ancash differs from *G. viridiflora* in its acute leaves and the glabrous corolla tube. *Gentianella poculifera* (Gilg) Zarucchi and *G. calcarea* (Gilg) J.S.Pringle, both from Junin, feature mostly acute, long pseudopetiolated basal leaves. The cauline leaves of the latter species are somewhat connate.

Cleistogamy:—Interestingly, possibly all green-flowered members of South American *Gentianella* so far described can be considered cleistogamous (see also Pringle 2012a). Our species does not seem to be an exception, as it was never found to be openly flowering during observation over a two week period whilst at the study site, with petals only found spreading once specimens had fruited (S.P. Sylvester, *pers. comm*.).

Etymology:—The specific epithet *viridiflora* refers to the green flowers of this new species.

Conservation status:—So far, *G. viridiflora* is known only from the type locality. As a consequence, there is no adequate information available on its distribution and population size, so *G. viridiflora* should be categorized as Data Deficient according to the IUCN Red List Categories and Criteria (IUCN 2001). Although large populations were encountered at the type locality, the likelihood that this species has its niche maintained by consistent heavy livestock grazing raises the question over its vulnerability to changing landuse, should a less intensive grazing scheme be employed.

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Chapter 10

The World's smallest Campanulaceae: *Lysipomia mitsii* sp.nov.

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Author contributions: S.P.S. & M.K. conceived the concept; S.P.S conducted the fieldwork; S.P.S. & L.A. performed herbarium taxonomy; D.Q. performed phylogenetic study; S.P.S., M.K. & D.Q. wrote the manuscript.

The World's smallest Campanulaceae: *Lysipomia mitsii* sp.nov.

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Abstract

Botanists and plant morphologists have long been fascinated by how certain species can exhibit such reduced morphologies that even their identification to genus- or family-level becomes difficult. Such was the case with *Lysipomia mitsii*, an exceptionally small plant discovered from the Peruvian Andes which bore characteristics of Campanulaceae but differed in size by an order of magnitude from the current smallest members known from the family and lacked diagnostic characters that would allow it to be reliably placed to genus-level. Molecular analyses of the *trnL-F* and ITS data, composed of a representative Campanulaceae sampling, clearly placed the sample within the genus *Lysipomia*, requiring that amendments be made to the description of the genus. The World's smallest Campanulaceae, *Lysipomia mitsii*, is thus described and illustrated with its systematic relationships to the other members of the genus being discussed. Its highly reduced morphology, which has given it status as the smallest Campanulaceae and, quite possibly, the World's smallest dicotyledoneous plant, is discussed in the light of current knowledge on the physiological and anatomical constraints on alpine plant growth and survival.

Keywords: alpine**;** Andes; bayesian analysis; dwarfism; Lobelioideae; smallest dicot

INTRODUCTION

The World's smallest angiosperms belong to the genus *Wolffia* Horkel ex Schleid. of the monocot family Araceae. However, within dicots there are a number of contenders for the title of 'smallest' species and, interestingly, the majority of these are found in high elevation habitats. The smallest dicot is commonly believed to be the dwarf mistletoe *Arceuthobium minutissimum* Hook. f., a leafless parasite of pine trees in the Himalayan altimontane zone measuring a mere 2-5 mm (Datta 1951). However, during plant surveys in the heavily grazed puna grasslands of the Cordillera Urubamba, southern Peru (Heitkamp & al. 2014), we discovered an annual autotrophic plant measuring just 1.8--4(--5.5) mm, that represents another contender for the World's smallest dicot.

The plants collected bore characteristics of Campanulaceae (e.g. connate Lobelioid-like androecium surrounding the style and adnate to the corolla tube, and inferior ovaries) but differed in size by an order of magnitude from the current smallest members known from the family. These diminutive plants exhibited a morphology that largely differed from the current generic circumscriptions, initially hampering a reliable generic placement based on morphological characters alone. Campanulaceae is a diverse family comprising 84 genera and c. 2400 species that occur in a vast array of habitats and exhibit a great diversity of life-forms ranging from dwarf herbs to 15 m tall trees (Lammers 2007; Antonelli 2008). Morphologically, our plants were most similar to species of the genus *Lysipomia*, but with several important differences. *Lysipomia*, until now, has been considered to comprise ca. 30--40 species of purely perennial low-rosulate cushion-forming herbs with congested alternate leaves that measure >10 mm and generally large (>3 mm), obviously bilabiate, flowers (Wimmer 1937, 1953; McVaugh

1955; Jeppesen 1981; Ayers 2000). The species introduced here is a diminutive annual with 'apparently' opposite leaves, due to the prominent cotyledons with rare occurrence of true leaves that measure <5 mm long, and small (<3.25 mm) flowers which are only faintly bilabiate. Within the Campanulaceae, *Lysipomia* is unique in possessing minute capsules that dehisce via an apical operculum (McVaugh 1955) with other delimiting characters including unilocular ovaries and non-resupinate flowers. Although the ovary was seen to be unilocular, it was difficult to discern the operculum as most encountered fruits were immature. Our species of *Lysipomia* also exhibited pseudoresupination, which added to the uncertainty surrounding generic delimitation of this species. To resolve the placement of this species within the Campanulaceae, we conducted a phylogenetic analysis to determine the systematic relationships of the plant and confirmed its placement within the genus *Lysipomia*.

In this paper we identify the generic placement and its relation within the genus of our new species of *Lysipomia* from the high-Andean Puna grasslands, using Bayesian inference and maximum likelihood analyses based on plastid *trnL-F* and nuclear ITS data. We describe and illustrate the new species, and present an up-to-date phylogeny for *Lysipomia*. We then discuss the systematic relationships of this new species to the other members of the genus and its highly reduced morphology, which gives it status as the World's smallest Campanulaceae.

MATERIALS AND METHODS

Molecular Phylogenetic Analyses. —

From the beginning it was clear that the plant material morphologically belonged to the Campanulaceae due to its distinct floral morphology, but its precise placement within the family was questionable. Therefore, we compiled a Campanulaceae backbone data set (see Appendix 1) from available *trnL-F* sequences in GenBank, including the *trnL*$_{UAA}$ group I intron and the *trnL-trnF* intergenic spacer (IGS), guided by Antonelli (2008). In agreement with an ample DNA-barcoding approach the nrITS region, including the internal transcribed spacers (ITS) 1 and 2 as well as the 5.8S gene of the nuclear ribosomal DNA (compare Wicke & al. 2011) complemented the plastid *trnL-F* region in order to pinpoint the relatedness of the sample. Fortunately, ITS sequence data for all known *Lysipomia* species was already present in GenBank from a study by Ayers (1999) that served as a basis for the ITS data set. Whole genomic DNA of the material was isolated using commercially available spin columns (NucleoSpin Plant II, Macherey-Nagel, Germany) following the manufacturer's protocol. Prior incubation with the lysis buffer plant material was pulverized in 2 ml Eppendorf caps (round bottom) containing 3 glass beads (5 mm) with a Mixer Mill (Retsch TissueLyser, Qiagen) at 30 Hz (two rounds of 1 min). PCR amplifications (T3 Thermocycler, Biometra) were performed in 25 µl-reactions containing 1 U Taq-DNA polymerase (GoTaq, Promega), 1 mM dNTP mix of each 0.25 mM, 1 x buffer, 1.25--2.5 mM $MgCl_2$ and 20 pmol of each amplification primer. PCR protocols for the *trnL-F* region followed Borsch & al. (2003). The ITS region was amplified using the primers ITS4 and ITS5 designed be White & al. (1990) with an amplification profile of: 5 min 94°C, 40 cycles (1 min 94°C, 1 min 48°C with a time-increment of +4s/cycle, 45 s 68°C) and a final extension of 7 min at 68°C. Column cleaned PCR products (NucleoSpinR Gel and PCR Cleanup, Macherey-Nagel, Germany) were sequenced by Macrogen Inc., South Korea (www.macrogen.com). Sequences were edited and aligned using PhyDE version 0.996 (available at http://www.phyde.de). Primer sequences were clipped off.

Maximum Likelihood (ML) reconstructions were done using RAxML (Stamatakis 2006) with the default settings in effect. Internal branch support was estimated by heuristic bootstrap

(BS) searches with 10,000 replicates each. Bayesian analyses were performed with MrBayes v3.2.3 (Ronquist & al. 2011), applying the GTR+Γ+I model. Four runs with four chains (5×10^6 generations each) were run simultaneously, with a chain sampling every 1000 generations. Tracer v1.4 (Rambaut & Drummond 2007) was used to examine the log likelihoods to determine the effective sampling size and stationary of the MCMC search. Calculations of the consensus tree, including clade posterior probability (PP) were performed based upon the trees sampled after the chains converged (< generation 500 000). Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph2 (Stöver & Muller 2010).

RESULTS

Taxonomic Treatment. —

Lysipomia mitsii S.P. Sylvester & D. Quandt **sp. nov.** (Fig. 1, 4A) — TYPE: PERU. Cuzco, Provincia Calca, Distrito Calca, grazed ground below the SW facing crags of the Laguna Yanacocha, 1.5 km E of Cancha Cancha village, Huarán, 4340 m, S13° 14' 28.4" W72° 01' 16.8", 27 March 2012, *S. P. Sylvester 1417* (Holotype: USM! Isotypes: K!, CUZ!, LPB!, Z!).

Diagnosis. – Differs from all other species of *Lysipomia* by being an extremely small annual less than 5.5 mm tall, with extremely small flowers <3.3 mm long, and leaves appearing opposite due to the prominent cotyledons, which measure 1--2.6(--5) mm long, and frequent absence of true leaves.

Minute glabrous annual herbs, 1.8--4(--5.5) mm tall. *Stems* 0.3--2 mm long. *Leaves* often composed of purely the cotyledons, sometimes 1 or 2 leaves are present above the cotyledons but appearing opposite due to the prominent cotyledons; *Cotyledons* subsessile, elliptic, 1--2.6(--5) mm long, 0.4--0.6 mm wide, slightly convex, apically obtuse, glabrous, marginally slightly thickened, slightly glassy, entire, the blades attenuate into short petioles much shorter than the blades, basally slightly broadened to sheathing; *Leaves* (if present) crowded and imbricate with the cotyledons, usually arising at 90° angle with the cotyledons so appearing decussate, subsessile, elliptic, usually shorter than the cotyledons, 0.5--1.5(--5) mm long, 0.25--0.5 mm wide, flat, apically obtuse, glabrous, marginally slightly thickened, slightly glassy, entire, the blades attenuate into short petioles much shorter than the blades, basally slightly broadened or not at all; *Flowers* pseudo-resupinate, 1(--3) per individual plant, 1.5--2.5(--3.3) mm long; Subsessile, pedicels 0.05--0.15 mm long; *Hypanthia* (and ovaries) turbinate, 0.5--0.95 mm long, surfaces smooth or minutely winged at ribs when dry; *Calyces* with lobes obtuse, subequal, the dorsal sepals 0.8--1.3 mm long, the others slightly shorter, the two ventral sepals 0.6--0.8 mm long, apices obtuse, margins entire, eglandular, persisting in fruit; *Corollae* white, tubes 0.5--0.8 mm long to the lateral sinuses, limbs faintly bilabiate, the lips presented horizontally or vertically facing the stem apices, the upper (dorsal) lobes broadly lanceolate, ca. 0.2 mm long, varying from slightly deflexed to incurved, the lower (ventral) lobes broadly lanceolate, ca. 0.1--0.18 mm long, varying from slightly deflexed to incurved; *Filament tubes* equal to corolla tubes; *Anthers* with tubes black, 0.2--0.3 mm long, not exerted from the corollae, the 2 lower anthers staminodial and present as hyaline lobes emerging ventrally from the stamen tubes, c.0.2 mm long; *Ovaries* turbinate, unilocular, placentation parietal, ovules in 2 rows inserted on a thin placental intrusion on the ventral surface. *Capsules* turbinate, ca. 1--2.2 mm long, (0.5--)1--1.5 mm wide, unilocular. *Seeds* ca. 8 per capsule, ovoid to slightly kidney shaped, narrowing slightly

to a prominent circular hilum, ca. 0.05 mm long, dark brown, with irregular longitudinal furrows and nearly smooth surface with indistinct cross-lines. Chromosome number unknown.

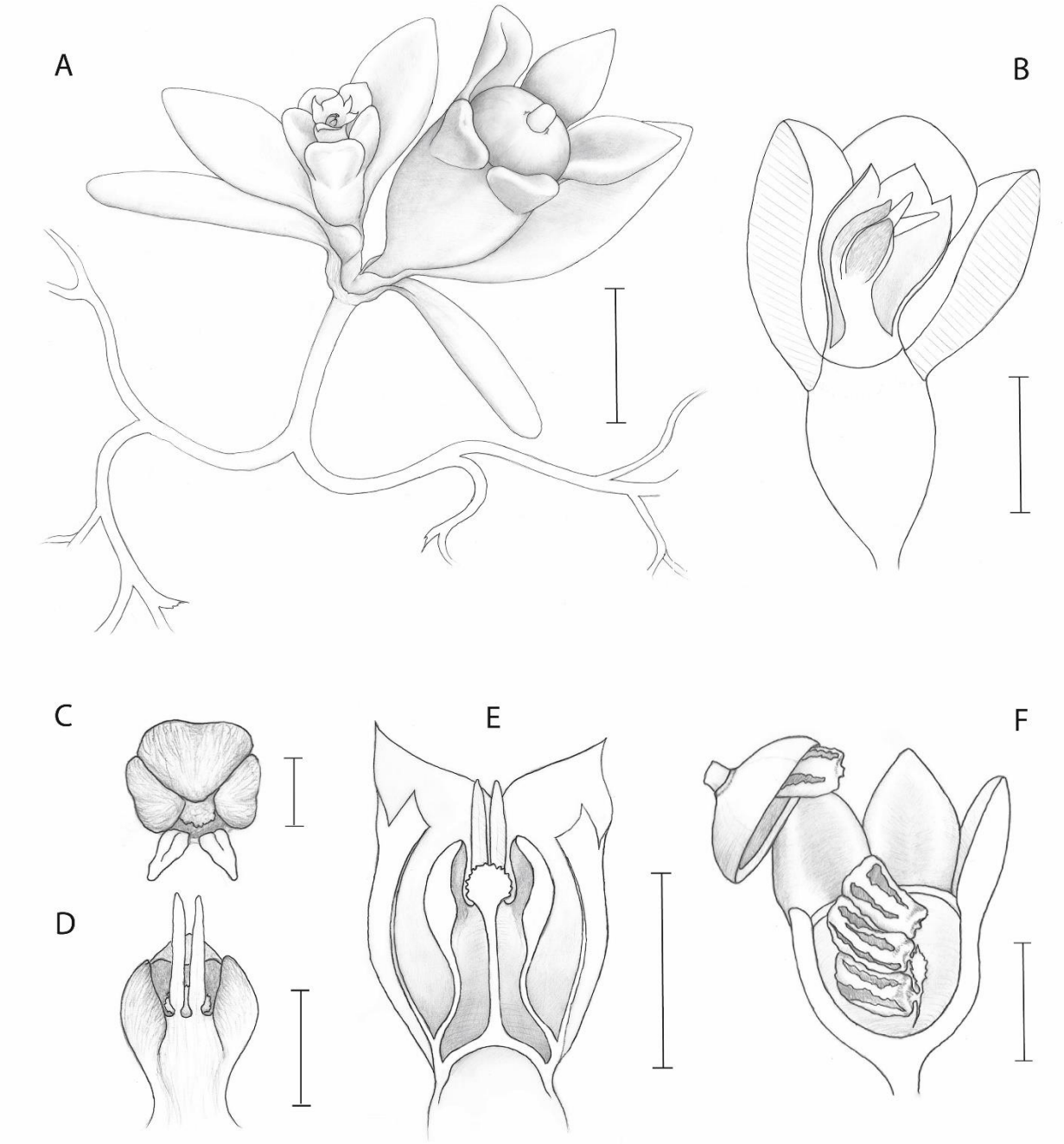

Fig. 1. *Lysipomia mitsii* S.P. Sylvester & D. Quandt. **A,** habit; **B,** side-view of a flower with the corolla and calyx removed to reveal the androecium; **C,** front view of the androecium, note the lower staminodial flap-like appendages; **D,** ventral view of the androecium with staminodial appendages in the foreground; **E,** longitudinal section of the corolla and androecium to reveal the style and stigma; **F,** longitudinal section of a fruit, showing the operculum and seeds attached to the thin placental intrusion on the ventral surface of the ovary. Measurement bars A,F = 1 mm, B,E = 0.5 mm, C,D = 0.2 mm. Illustrations by Lolita Ammann.

Ecology and Distribution. – Locally abundant and common on bare ground open to sunlight in heavily grazed puna grassland. Up to 500 individual plants were encountered in a single $2x2m^2$ plot studied at the type locality and indicator species analyses have retrieved this species as a significant indicator species of grazed puna grassland (Sylvester et al. *unpubl. data*). The plants were found to root in a hardened organic soil crust and were found associated with mosses, lichens and other low-growing plants such as *Agrostis breviculmis* Hitchc., *Azorella biloba* (Schltdl.) Wedd. and *Lachemilla pinnata* (Ruiz & Pav.) Rothm. The species is currently known only from two sites in the same valley, although collections were made from only one of these sites. The other site where the species was recorded, but not collected, was 5 km NE of Huarán on the NW facing slope found to the immediate N of the prominent tower known by locals as "Kontorqayku", S13° 16' 02.6" W72° 01' 12.9", c. 4300 m. This species is the second *Lysipomia* to be noted as endemic for Peru (Leon & Lammers 2006). However, the extent of its distribution is unclear as it is likely to have gone unnoticed by botanists until now and may occur in other areas of Peru.

Etymology. – The name refers to the beloved wife of the first author, Mitsy D.P.V. Sylvester, who was an invaluable help during vegetation surveys and was the first to spot this minute species. It is not nearly as cute.

Additional specimens examined. – PERU. Cuzco, Provincia Calca, Distrito Calca, grazed ground on the flat pampa 100 m W of Laguna Yanacocha, close to the settlements, 1.5 km E of Cancha Cancha village, Huarán, 4314 m, S13° 14' 13.4" W72° 01' 06.3", 22 March 2011, *S. P. Sylvester 823* (CUZ, Z).

Comments. – This species can be easily separated from all other members of the genus by its annual habit, small stature, and small leaves and flowers. There are a few species of *Lysipomia* with relatively small flowers that all belong to subgenus *Lysipomia*, e.g. *L. crassomarginata* (E. Wimm.) Jeppesen, *L. montioides* Kunth, *L. muscoides* Hook. and *L. sphagnophila* Griseb. ex Wedd., but all these differ from *L. mitsii* by being obviously perennial, cushion forming and generally larger. The smallest member of the genus, apart from *L. mitsii*, is likely to belong to the *L. sphagnophila* complex, with specimens quoted forming cushions 1 cm high and 1--1.5 cm in diameter with flowers 2--2.5 mm long (Jepperson 1981). The fact that it is the smallest member of the Campanulaceae by at least an order of magnitude from the smallest other members, also belonging to *Lysipomia*, means that it would be difficult to mistake for any other genus within the family.

Molecular Phylogenetic Analyses. — The *trnL-F* backbone analyses of the Campanulaceae clearly identify the probe as a member of the genus *Lysipomia* and sister to *Lysipomia sphagnophila* with maximum support (Fig. 2). Although both species share several unique sequence characteristics such as various joint indels (>5nt up to 18nt), they are also conspicuously different (p-dist = 1.9%) with a distinguishing repeat (6 nt) in *Lysipomia sphagnophila* as well as a 5 nt indel in L *Lysipomia mitsii.* A more detailed analysis of the intrageneric relationships based on the ITS data converges to the same scenario with both species clustering together, although considerably less supported compared to the plastid tree (Fig. 3). This is reflected by the considerable sequence divergence (p-dist = 5.8) and two big indels

> 10 nt. Thus, although *Lysipomia sphagnophila* seems to be the sister species in the current species sampling, genetic differentiation is as high as the morphological divergence.

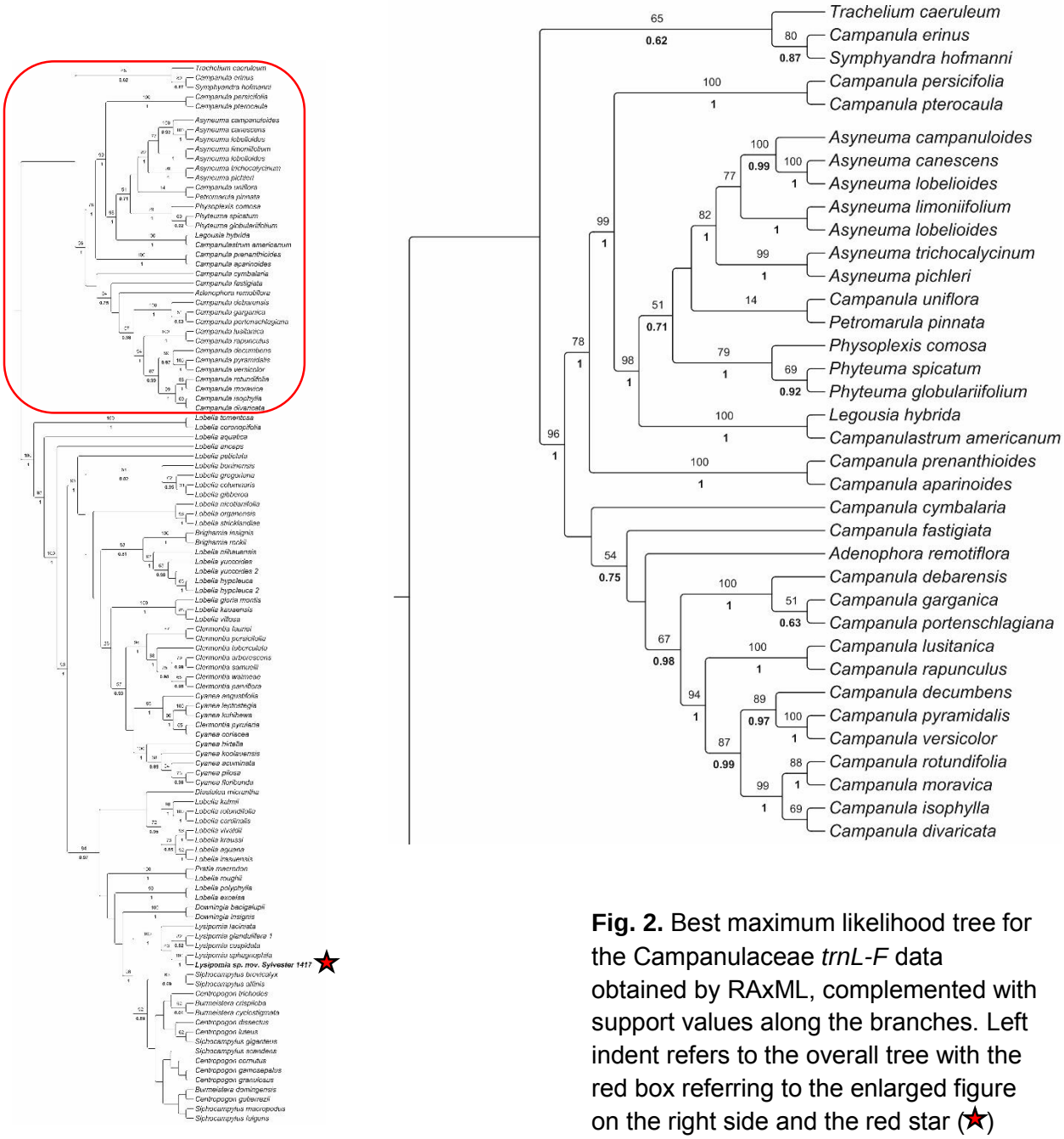

Fig. 2. Best maximum likelihood tree for the Campanulaceae *trnL-F* data obtained by RAxML, complemented with support values along the branches. Left indent refers to the overall tree with the red box referring to the enlarged figure on the right side and the red star (★) referring to the position of *Lysipomia mitsii*. Maximum likelihood bootstrap support is shown above the branches, while posterior probabilities are shown below in bold.

Fig. 2. Continued.

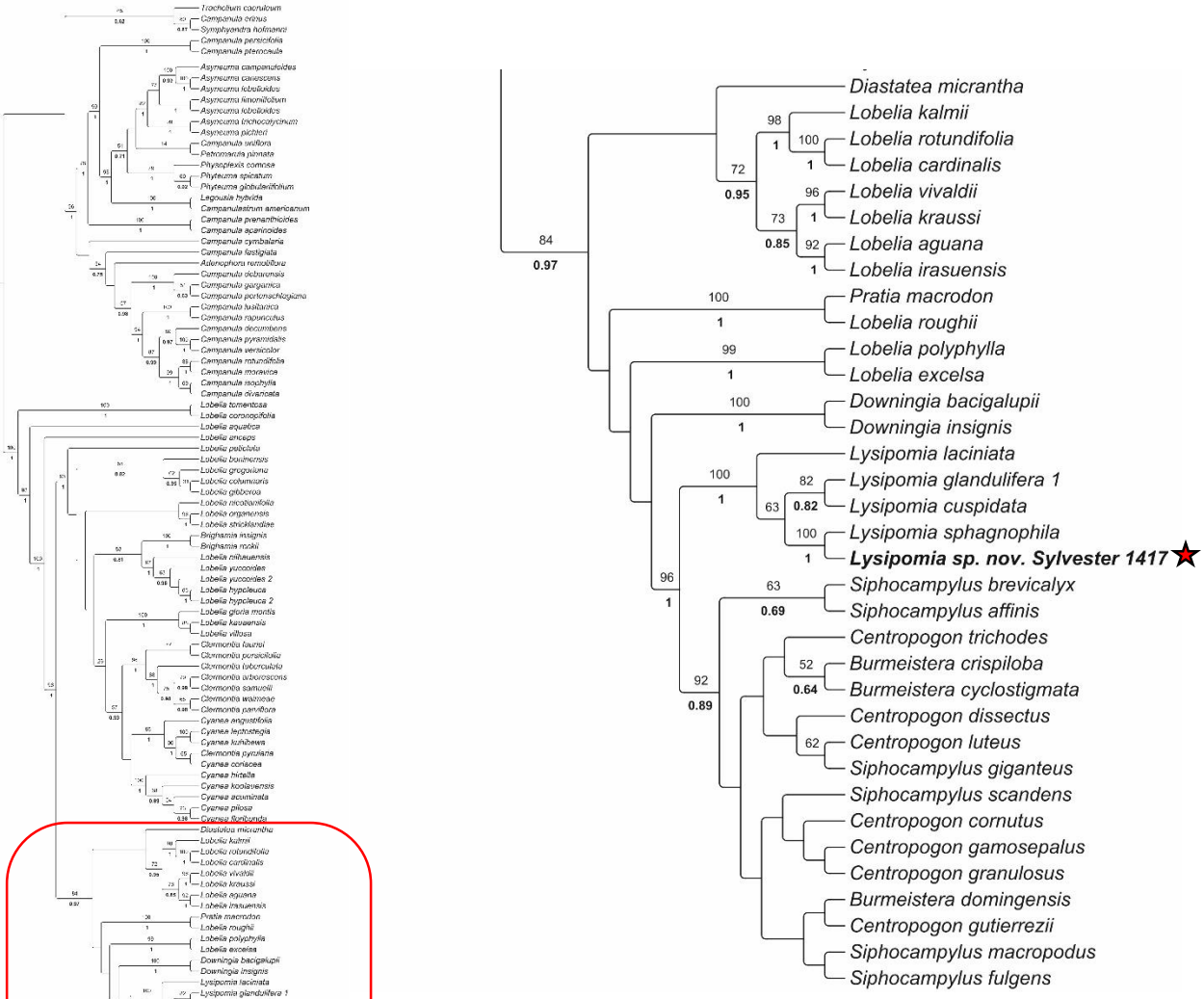

Fig. 2. Continued.

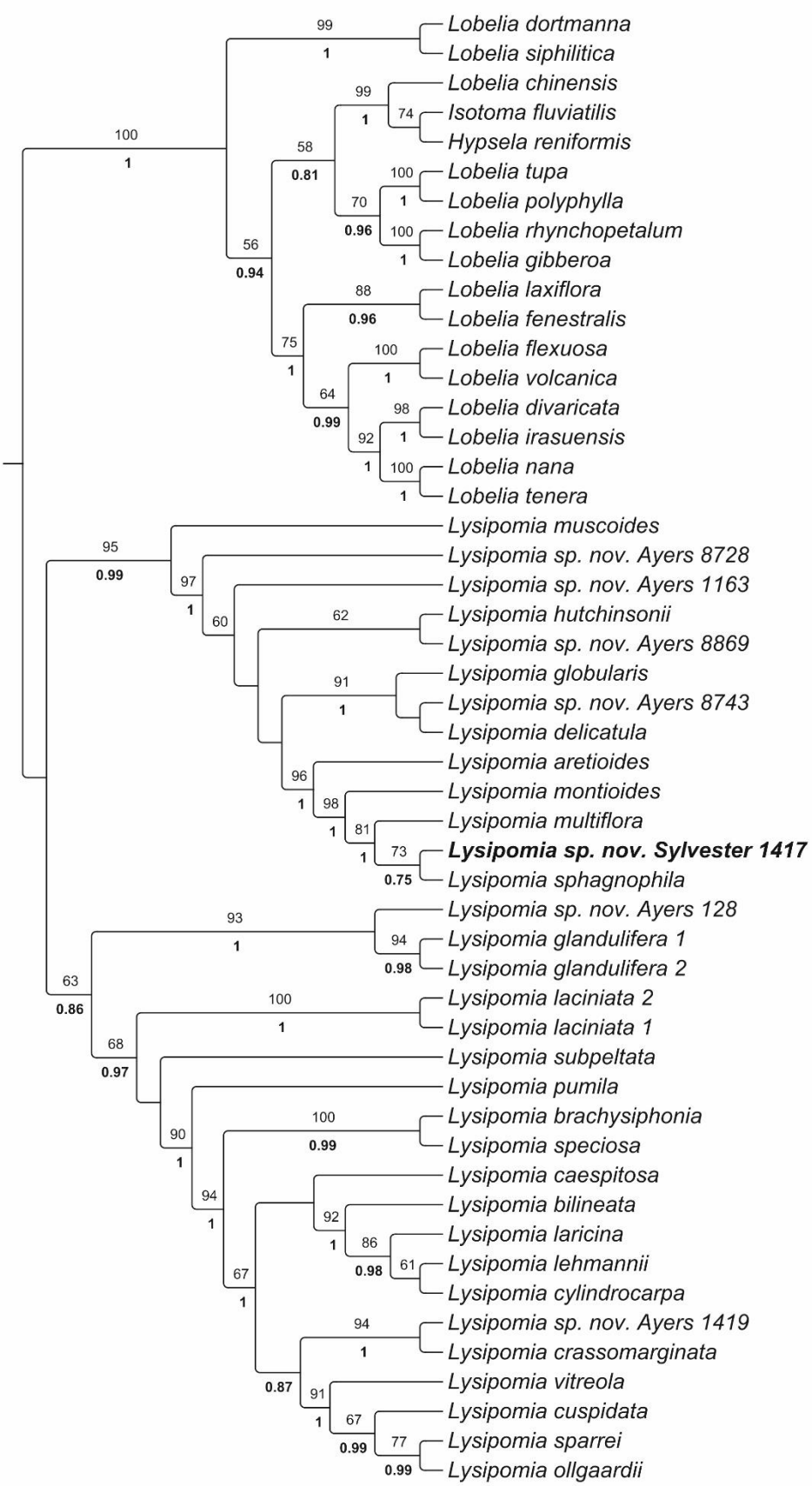

Fig. 3. Best maximum likelihood tree for the *Lysipomia* ITS data obtained by RAxML, complemented with support values along the branches. Maximum likelihood bootstrap support is shown above the branches, while posterior probabilities are shown below in bold.

DISCUSSION

Morphological delimitation of *Lysipomia.* —
The main characters that delimit *Lysipomia*, i.e., possession of minute capsules that dehisce via an apical operculum and unilocular ovaries with ventral parietal placentation, were still retained in this minute member of the genus. Currently, the genus *Lysipomia* is further characterized as short, perennial herbs with alternate leaves, spirally arranged or in terminal rosettes. Flowers are either crowded and terminal or solitary in leaf axils, non-resupinate (although pseudoresupination is common in the genus; Ayers 1997), and with a typically lobelioid corolla and androecium, the androecium containing 5 connate stamens (Wimmer 1937, 1953; McVaugh 1955; Jeppesen 1981). Because of the differing morphology of *Lysipomia mitsii* from other members of the genus, a recircumscription of the genus *Lysipomia* is required to include the following unique characters: annual habit, opposite leaves (referring to cotyledons), and a reduction of stamen number from 5 to 3. The reduced size of the flower has led, understandably, to this species being the first member of *Lysipomia* to exhibit floral reduction with the loss of two of the anthers that have been replaced by staminodial flap-like appendages. Other members of *Lysipomia* and other lobelioid genera have bristle-like appendages emerging from the ventral anthers and it has been suggested that these appendages function in pollen dispersal, although the direct mechanism involved remains unclear (Peter Endress *pers. comm*.).

Phylogenetic Relationships within *Lysipomia.* —
Lysipomia is considered to be monophyletic, and is sister to a group comprising the Neotropical shrubs *Burmeistera*, *Centropogon* and *Siphocampylus* (Antonelli 2008, 2009; Knox & al. 2008). The genus has been traditionally separated into subgenera *Lysipomia* and *Rhizocephalum*, with Wimmers (1953) brief revision separating the subgenera based on corolla morphology and anther insertion. McVaugh (1955) produced the only detailed revision of the entire genus and separated *L. laciniata* and *L. pumila* from all other species, placing them in subgen. *Rhizocephalum,* based on their acaulescent habit and thick fleshy roots arising from a corm-like stem. This was then superseded by Ayers (1999) who used cladistic analyses of morphology, anatomy and nrITS DNA data from 30 species (7 of which were undescribed species new to science) to recognize the two subgenera based on characters of flower size and colour. Subgenus *Rhizocephalum* was seen to contain species with large flowers and nectar guides, whereas subgenus *Lysipomia* contained species with small flowers that lack nectar guides. Interestingly, the southern and most widespread species of subgenus *Rhizocephalum*, *L. laciniata* and *L. pumila*, were suggested to be basally diverging (Ayers 1999; Price & Ayers 2008). This observation, coupled with results from area cladograms (Ayers 1999), allowed the postulation that the subgenus *Rhizocephalum*, and perhaps the entire genus, originated in southern Peru or Bolivia and that the diversity seen in the northern Andes is a product of repeated dispersal events from the south (Ayers 1999). Subgenus *Lysipomia*, on the other hand, was hypothesised to have its origin in the mountains south of the Huancabamba depression as most species are found to occur south of the depression with the Rio Marańon forming an effective barrier to separate sister species (Ayers 1999).

Our analysis produced a phylogeny similar to that of Ayers (1999) with *Lysipomia* being split into two large subdivisions, considered as subgenera *Rhizocephalum* and *Lysipomia*, which can be separated based on characters of flower size and colour with subgen. *Rhizocephalum* containing species with large corollas and nectar guides. Not surprisingly, *L. mitsii* is found to be nested within subgenus *Lysipomia* characterized by small flowers with corollas that lack nectar guides.

Lysipomia mitsii is placed as sister to *L. sphagnophila*, which coincidentally includes subspecies previously considered the smallest members of the genus. These two species are seen to be the most derived in subgenus *Lysipomia.* Interestingly, *L. sphagnophila* is the only widespread species of subgenus *Lysipomia*, being found from Venezuela to Bolivia, and comprises many infraspecific taxa (McVaugh 1955; Jeppesen 1981). One may speculate that it is the progenitor or parent species from which *L. mitsii* evolved. From extensive field collections (S.P. Sylvester *unpubl. data*), herbarium work, and literature (McVaugh 1955) we can ascertain that the *L. sphagnophila* found in the Cusco region is subsp. *sphagnophila* so it may be assumed that *L. mitsii* is derived from this taxon.

The topology of the ITS tree generated has large differences from that of Ayers (1999) with subgenus *Lysipomia* being generally a grade with some small clades embedded within whilst Ayers (1999) retrieved two large clades. Most likely, this reflects that Ayers combined both molecular and morphological as well as anatomical data in the phylogenetic reconstructions. For example, Ayers (1999) considered *L. muscoides* to be sister to *L. delicatula* whilst our results suggest that *L. muscoides* is basally diverging within the subgenus and is distantly related to *L. delicatula*. *Lysipomia laciniata* and *L. pumila*, grouped by Ayers (1999) and considered to be basally diverging in subgenus *Rhizocephalum* (Ayers 1999; Price & Ayers 2008), are not supported as sister taxa or seen as being basally diverging in our study. Instead, these species form part of a grade in the subgenus *Rhizocephalum* with *L. subpeltata* being nested between them. Affinities of *L. laciniata* and *L. pumila* have been previously asserted through morphological and anatomical studies with these species being considered distinct due to a) 3 colpate pollen as opposed to 6 colpate pollen in all other taxa, b) vertical, disk-like stems and c) the presence of contractile roots (Price & Ayers 2008). Our results imply that these characters are not ancestral plesiomorphic character states but, instead, derived character states. Our phylogeny supports *L. glandulifera* and *Lysipomia* sp. nov. (Ayers 128) as being basally diverging in the subgenus *Rhizocephalum*. As *L. glandulifera* is restricted to southern Peru and Bolivia, this still provides support for Ayers (1999) hypothesis over a southern origin for subgen. *Rhizocephalum.*

The phylogeny of *Lysipomia* produced by Madriñán & al. (2013, *supp. mat*.) differed largely from ours or that of Ayers (1999), with no distinct grouping of the taxa into two large subgenera being made. Madriñán & al. (2013) do not mention in detail how they constructed their phylogeny and so the cause of these differences in topology remains unclear.

Ecology of the World's smallest Campanulaceae. —

The genus *Lysipomia* contains ca. 30--40 species endemic to the high Andes, inhabiting paramo and humid puna grasslands above 3000 m with most species considered to be narrow endemics, often restricted to a single ridge or volcanic cone (McVaugh 1955; Ayers 1997; Lammers 2007; Price & Ayers 2008). The genus has been found to have a high net diversification rate and contributes to the high Andean paramo being considered 'the world's fastest evolving and coolest biodiversity hotspot' (Madriñán & al. 2013). The majority of *Lysipomia* species are found in the northern Andes, extending from Venezuela to northern Peru, where the highest diversity is found on both sides of the Amotape-Huancabamba zone (Luteyn 1999; Sklenar & al. 2011). Interestingly, our species of *Lysipomia* is found in fairly dry puna vegetation of southern Peru. Only four other species, *L. glandulifera, L. laciniata*, *L. pumila* and *L. sphagnophila,* are

known from southern Peru and Bolivia but these are found from humid puna vegetation (Brako & Zarucchi 1993; Jørgensen & al. 2014; Tropicos.org 2015).

Lysipomia mitsii is found growing in biological soil crusts in high elevation puna grasslands of the central Andes. The species is adapted to a nutrient poor, overgrazed, exposed habitat (Fig. 4B) where it has to face challenges of aluminium toxicity in the soils and mean daily temperature oscillations ranging by 24 K with daily mean minimum temperatures being -1.7°C (Heitkamp & al. 2014: 18). The climate was notably drier compared to sites where other members of *Lysipomia* occur (S.P. Sylvester *unpubl. data*) and may reflect adaptations of *L. mitsii* to drier environments, possibly through its annual lifecycle. The exceptionally small size of the plant, coupled with the harsh climate experienced by these high elevation grasslands (for climatic data see Heitkamp & al. 2014: 18) opens up a plethora of questions regarding the physiological capacity of plants to survive in extreme environments. The discovery of this unusual plant should spur further research to discern what limitations govern alpine plant growth and survival.

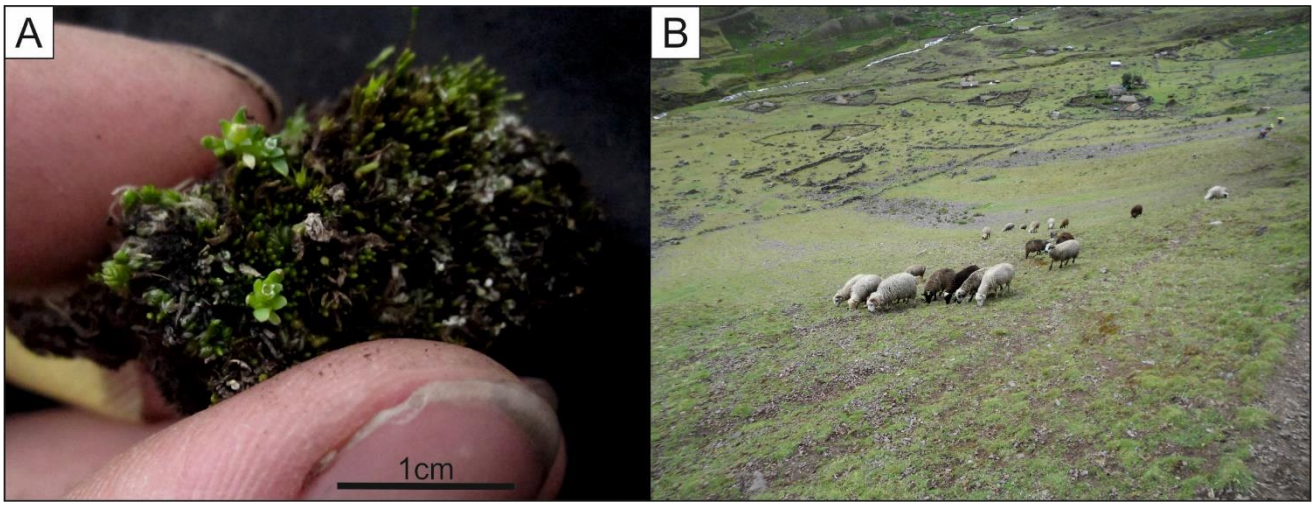

Fig. 4. A, *Lysipomia mitsii* showing fruiting and flowering specimens; **B,** Habitat of *L. mitsii*: heavily grazed puna grassland — Photo A by S.P. Sylvester; B by F. Heitkamp.

Argument could arise over whether this species is phenotypically, rather than genotypically, small and that its reduced size could be a response to drought, nutrient shortage, high light stress or lower temperature (Körner & Pelaez Menendez-Riedl 1989) and, under more favourable conditions, it would grow much larger. Dwarfism has been documented from different alpine areas (e.g. Shinohara & Murakami 2006; Körner 2003) but, in the case of *L. mitsii*, no larger individuals of have been discovered at lower elevations of the study area or in local herbaria (CUZ, LPB, USM). We would argue that this species is at its ecological optimum but that it occupies a very narrow ecological niche that is maintained by heavy grazing and harsh conditions and that, under more favourable conditions, it would be outcompeted by other forbs. This assumption is supported by how *L. mitsii* was not noted from areas with reduced grazing which probably reflects competition by tussock grasses for light in less disturbed habitats. Furthermore, all individuals of *L. mitsii* were found either flowering or fruiting which suggests that these are source populations, as opposed to sink populations of subalpine species that can barely tolerate the harsh and stressful open alpine habitat. The likelihood that this species has its niche maintained by consistent heavy livestock grazing raises the question over its vulnerability

to changing landuse, should a less intensive grazing scheme be employed. On the other hand, it also raises the question as to the natural habitat of the species in the absence of human pastoral activities.

Could this be the World's smallest dicotyledonous plant? —
Following a literature search of all species belonging to Campanulaceae, none were found with a habit as diminutive as *L. mitsii*. This exceptionally small plant quite evidently holds the record for the World's smallest Campanulaceae and, quite possibly, the World's smallest dicot. Within the dicots, the current record for smallest species is held by *Arceuthobium minutissimum,* a leafless aclorophyllous parasitic mistletoe measuring 2--5 mm, minus the haustoria (Datta 1951). There are a number of other 'autotrophic' contenders for the title of 'smallest' dicotyledoneous species and, interestingly, the majority of these are found in the high elevation grasslands and tundra of the Andes. The central and southern high Andes seem to be a 'hotspot' for miniscule plants with the recent discovery of the aptly named *Viola lilliputana* Ballard & Itlis (2012) from Peru, and miniscule members of *Oxalis, Geranium, Crassula, Draba* etc. being mentioned by Körner (2003: 236) from Argentina. Other small annual species such as *Crassula closiana* (Gay) Reiche and *Cicendia quadrangularis* (Dombey ex Lam.) Griseb. were also found growing alongside *Lysipomia mitsii* on open, bare ground. However, none have thus far been found which are smaller than *Lysipomia mitsii* in terms of height and overall body size, although a much more exhaustive literature search would be needed to verify the claim for a World record.

Perhaps more interesting than the question regarding which individual plant species might be smallest, is the fact that it appears several dicots have independently reached a size of 2--5 mm. Could it be that this is the minimum size physiologically possible for homoiohydric land plants? A similar situation is well known among warm-blooded vertebrates, where a minimum body mass of ca. 2 g, determined by physiological constraints of energy uptake and loss, has independently been reached in birds and mammals (Fons & al. 1997; Schuchmann 1999; Norberg & Norberg 2012). Among plants, it is striking that, when water is not limiting, plants become much smaller than 2 mm. In the aquatic realm, examples are *Wolffia,* among the angiosperms, and the much smaller aquatic algae. On land, poikilohydric plants include bryophytes less than 1 mm in size (e.g., epiphyllous Lejeuneaceae) and much smaller minute algae. For homoiohydric plants that need to take up, transport and store water, there may be physical and anatomical constraints that would not allow a plant to have roots, stems and leaves below a certain minimum size. *Lysipomia mitsii* and other such minute species may have reached this limit and, as such, might provide interesting insights into the limitations of plant size at the lower end of the size spectrum.

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Appendix 1

GenBank accession numbers for the downloaded *trnL-F* sequences of the Campanulaceae backbone data set (species, Accession number;)

Asyneuma campanuloides, FJ426570; *Asyneuma canescens*, FJ426567; *Asyneuma limoniifolium*, FJ426571; *Asyneuma lobelioides*, EF088695; *Asyneuma lobelioides*, FJ426568; *Asyneuma trichocalycinum*, FJ426566; *Asyneuma pichleri*, FJ426569; *Campanula uniflora*, FJ426574; *Campanulastrum americanum*, EF088776; *Legousia hybrida*, EF088783; *Physoplexis comosa*, FJ426586; *Petromarula pinnata*, FJ426585; *Phyteuma spicatum*, EF088787; *Phyteuma globulariifolium*, FJ426582; *Campanula persicifolia*, FJ426573; *Campanula pterocaula*, EF088751; *Campanula divaricata*, EF088718; *Campanula isophylla*, FJ426583; *Campanula rotundifolia*, EF088759; *Campanula moravica*, EF088740; *Campanula garganica*, FJ426581; *Campanula portenschlagiana*, FJ426587; *Campanula debarensis*, FJ426575; *Campanula decumbens*, EF088716; *Campanula lusitanica*, EF088733; *Campanula rapunculus*, EF088758; *Campanula versicolor*, FJ426591; *Campanula pyramidalis*, EF088754; *Adenophora remotiflora*, EF088693; *Campanula cymbalaria*, EF088715; *Campanula erinus*, EF088720; *Trachelium caeruleum*, EF088791; *Symphyandra hofmanni*, EF088727; *Campanula fastigiata*, EF088721; *Campanula aparinoides*, EF088702; *Campanula prenanthioides*, EF088748; *Lysipomia sphagnophila*, DQ356197; *Lysipomia cuspidata*, DQ356198; *Lobelia gregoriana*, DQ356187; *Lobelia stricklandiae*, DQ356186; *Lobelia anceps*, DQ356184; *Lobelia aquatica*, DQ356182; *Lobelia coronopifolia*, DQ356181; *Lobelia tomentosa*, DQ356180; *Lobelia kraussi*, DQ356179; *Lobelia rotundifolia*, DQ356178; *Lobelia polyphylla*, DQ356177; *Lobelia cardinalis*, DQ285168; *Lobelia vivaldii*, DQ285167; *Lobelia aguana*, DQ356176; *Lobelia irasuensis*, DQ356175; *Lobelia villosa*, DQ285176; *Lobelia petiolata*, DQ285163; *Lobelia columnaris*, DQ285158; *Lobelia boninensis*, DQ285157; *Lobelia organensis*, DQ285162; *Lobelia nicotianifolia*, DQ285161; *Lobelia gibberoa*, DQ285160; *Lobelia hypoleuca*, DQ356191; *Lobelia yuccoides*, DQ356190; *Lobelia yuccoides*, DQ285152; *Lobelia niihauensis*, DQ285151; *Lobelia hypoleuca*, DQ285149; *Lobelia kauaensis*, DQ285150; *Lobelia gloria-montis*, DQ285148; *Pratia macrodon*, AY568753&AY568742; *Burmeistera domingensis*, DQ356214; *Lobelia excelsa*, DQ285159; *Burmeistera crispiloba*, DQ285164; *Siphocampylus brevicalyx*, DQ356224; *Lobelia roughii*, EF126737; *Lobelia kalmii*, EF126736; *Burmeistera cyclostigmata*, DQ356213; *Siphocampylus fulgens*, DQ356216; *Siphocampylus affinis*, DQ356223; *Siphocampylus giganteus*, DQ356222; *Siphocampylus macropodus*, DQ356221; *Siphocampylus scandens*, DQ356218; *Centropogon cornutus*, DQ356226; *Centropogon gamosepalus*, DQ356225; *Centropogon granulosus*, DQ356220; *Centropogon luteus*, DQ356219; *Centropogon trichodes*, DQ356217; *Centropogon dissectus*, DQ356215; *Downingia bacigalupii*, DQ356183; *Downingia insignis*, DQ356185; *Diastatea micrantha*, DQ356203; *Centropogon gutierrezii*, DQ285165; *Cyanea koolauensis*, DQ356193; *Brighamia insignis*, DQ356189; *Brighamia rockii*, DQ285140; *Cyanea hirtella*, DQ285175; *Cyanea pilosa*, DQ285174; *Cyanea kuhihewa*, DQ285177; *Cyanea angustifolia*, DQ356173; *Cyanea leptostegia*, DQ285172; *Cyanea coriacea*, DQ285145; *Cyanea floribunda*, DQ285173; *Cyanea acuminata*, DQ285144; *Clermontia waimeae*, KC460653; *Clermontia parviflora*, DQ285171; *Clermontia arborescens*, DQ285141; *Clermontia fauriei*, DQ285142; *Clermontia samuelii*, KC460651; *Clermontia tuberculata*, KC460652; *Clermontia pyrularia*, KC460650; *Clermontia persicifolia*, KC460649;

Generated *trnL-F* sequences (species, isolate, Herbarium:voucher (duplicates in), Accession number is being processed in Genbank):

Lysipomia mitsii, ED884, Z:Sylvester 1417 (CUZ, LPB); *Lysipomia glandulifera*, ED1101, Z**:**Sylvester 1891 (LPB); *Lysipomia laciniata*, ED1100, Z:Sylvester 213 (CUZ).

GenBank accession numbers for the downloaded ITS1&2 sequences of the *Lysipomia* backbone data set (species, Accession number;)

Lysipomia delicatula, AF054957; *Lysipomia globularis,* AF054955; *Lysipomia sp. nov. 1163* , AF054966; *Lysipomia sp. nov. 8743* , AF054967; *Lysipomia muscoides,* AF054948; *Lysipomia hutchinsonii,* AF054954; *Lysipomia sp. nov. 8869,* AF054969; *Lysipomia sp. nov. 8728,* AF054965; *Lysipomia montioides,* AF054950; *Lysipomia sphagnophila,* AF054943; *Lysipomia multiflora,* AF054949; *Lysipomia aretioides,* AF054964; *Lysipomia cuspidata,* AF054959; *Lysipomia ollgaardii,* AF054947; *Lysipomia sparrei,* AF054945; *Lysipomia vitreola,* AF054939; *Lysipomia crassomarginata,* AF054960; *Lysipomia sp. nov. 1419,* AF054968; *Lysipomia brachysiphonia,* AF054962; *Lysipomia pumila,* AF054946; *Lysipomia speciosa,* AF054944; *Lysipomia caespitosa,* AF054961; *Lysipomia bilineata,* AF054963; *Lysipomia cylindrocarpa,* AF054958; *Lysipomia laricina,* AF054952; *Lysipomia lehmannii,* AF054951; *Lysipomia laciniata 1,* AF054953; *Lysipomia subpeltata,* AF054942; *Lysipomia glandulifera,* AF054956; *Lysipomia sp. nov. 128,* AF054940; *Lobelia flexuosa,* AY350626; *Lobelia volcanica,* AY350625; *Lobelia nana,* AY350629; *Lobelia tenera,* AF054938 AF054938; *Lobelia irasuensis,* AY362765; *Lobelia divaricata,* AY362764; *Lobelia siphilitica,* DQ006015; *Lobelia dortmanna,* EU219388; *Lobelia fenestralis,* AY350634; *Lobelia laxiflora,* AY350631; *Lobelia polyphylla,* AY350633; *Lobelia tupa,* AY350632; *Isotoma fluviatilis,* AY644648; *Hypsela reniformis 2,* AF054941; *Lobelia chinensis,* KM051440; *Lobelia rhynchopetalum,* FJ664109; *Lobelia gibberoa,* EU219380;

Generated ITS sequences (species, isolate, Herbarium:voucher (duplicates in), Accession number;):

Lysipomia mitsii, ED884, Z:Sylvester 1417 (CUZ, LPB); *Lysipomia glandulifera*, ED1101, Z**:**Sylvester 1891 (LPB); *Lysipomia laciniata*, ED1100, Z:Sylvester 213 (CUZ).

OUTLOOK AND FUTURE RESEARCH

This research shows us clearly that baseline data, based on current ecological conditions, is crucial for evaluating the effect of anthropogenic disturbance on ecosystem properties and processes. Furthermore, it highlights that caution should be taken when attempting to quantify anthropogenic perturbation on ecosystems in the absence of this baseline data as properties and processes forming natural ecosystems can be wholly unpredictable and knowledge of human impact on ecosystem properties will be fundamentally biased until we are able to obtain baseline data from pristine ecosystems. Likewise, caution should also be taken when applying conservation measures or restoration goals in the absence of this baseline data.

Our research also exemplifies the largely contrasting effects of human disturbance at local and landscape scales. At local scales, as in chapters 1 and 2 and local-scale data from chapter 3, human influence can be seen to have relatively positive effects, creating higher alpha diversity through disturbance opening up many ecological niches whilst there being little effect on soil nutrients and overall carbon stocks. At the landscape scale shown in chapter 3, the picture is completely different, with human influence seen to reduce regional plant diversity through homogenization by favouring widespread generalist species at the expense of ecosystem specialists. Human disturbance was also seen to cause massive changes in vegetation cover which influences soil properties and carbon stocks but, despite the huge reduction in forest cover, carbon stocks were seen to be relatively little affected due to higher SOC storage in grasslands. Taking these differences into account, our study suggests that moderate levels of land use are likely to be compatible with biodiversity, soil and carbon conservation at the regional level. These baselines have far-reaching implications for our understanding of human impact on ecosystems and their influence on paleoclimatic modelling (Kaplan et al. 2011) as well as our understanding of previous and potential biodiversity distributions.

Much can still be done with the data that we collected from the Andes. Studies looking at vegetation properties in more depth, covering things such as beta partitioning (e.g. Lozada et al. 2008), geographic floral elements and chorology of the natural vs. disturbed vegetation (e.g. Sklenář et al. 2011; Sklenář & Balslev 2007), could still be done. A general phytosociological treatment that describes, in detail, the potential natural vegetation of these sites and the surrounding disturbed landscapes, in combination with the aforementioned research possibilities, would be valuable additions to future research on these ecosystems. Data from the large number of soil profiles, and plot data on vascular plants associated to each soil profile, could also be analysed to assess how soil properties influence vegetation composition on a much finer scale. It seems that grazing and burning are the overriding factors determining species composition in disturbed ecosystems, as the same species can be found regardless of the microclimate and soil type in which they grow. If we were to prove this empirically, this would further our knowledge on how human influence homogenises vegetation (McKinney & Lockwood 1999).

Now that we have established that the natural vegetation in our study area is a mosaic of *Polylepis* - *Gynoxys* forest and tussock grassland, the question arises over what determines this mosaic-like vegetation structure. Certain research has found that negative moisture balance and waterlogging are critical in determining the niche space available for *Polylepis* (Bader & Ruitgen 2008; Gosling et al. 2009). It is likely that factors such as topography, microclimate and soil attributes, all interact to either limit or promote tree establishment in the natural Puna ecosystem. Current research aiming to deduce the factors

affecting natural *Polylepis* woodland distribution is confounded by the inability to control for anthropogenic impact, making it difficult to tease apart what natural processes allow the establishment of forests. My novel approach, using mountaineering techniques to access pristine vegetation, offers a unique opportunity to perform natural experiments to test these questions.

Another question that arises is, if the natural vegetation of the Andes comprises a majority of species with no adaptations to fire or grazing, then where has the widespread prevalent vegetation, with species adapted to burning and grazing, come from? 13,000 years of human disturbance is not enough time for the high diversity of grazing/burning adapted plants, now seen across these landscapes, to have evolved. This implies that these species must have been present in the natural vegetation, but in much smaller amounts, probably restricted to areas of disturbance such as landslides, animal burrows etc.. Then with the arrival of humans, widespread disturbance through burning of the vegetation and livestock grazing, opened up the available niche space of these species allowing them to become common and widespread. I encountered this scenario (i.e. plants common in disturbed areas being found in disturbed azonal vegetation) in the pristine areas of the study sites but did not specifically focus on this or collect data from these parts of the vegetation as my fieldwork was focussed on zonal vegetation. It would be interesting to expand the study and test where the grazing and burning adapted vegetation would belong within natural ecosystems. This would give us a better notion of how humans have affected natural habitats. Interestingly, there is a large expanse of wilderness in the Cordillera Vilcabamba that is reported to be pristine and untouched by human activity with a few preliminary expeditions to the area encountering many undescribed species and documenting a *Polylepis* forest-grassland mosaic in higher elevation areas (Brooks Baekeland 1964; Alonso et al. 2001). One brilliant idea for a future project would be to access this pristine wilderness and study both zonal and azonal ecosystems to see which type of habitat the common widespread autochthonous grazing- or fire-adapted species would be associated with.

With all this interesting data gathered from the high Andes, another idea now is to see whether these patterns and processes in vegetation and soil development, often differing from preconceived ideas, also hold true for other high mountain ecosystems such as the Himalaya. Reinhold Messner, Drs. Georg and Sabine Miehe (Philipps-Universität Marburg) and Dr. Colin Pendry (Royal Botanic Garden of Edinburgh) have confirmed existence of inaccessible zonal vegetation in difficult-to-access valleys of the Khumbu region of Eastern Nepal. I am now seeking funding to organize an expedition to these sites whereupon I will use a similar methodology to that of the Andes to see whether there is a general consistent response in high mountain vegetation and soil development to human disturbance at a global level.

Our data also have important implications for treeline ecology. The upper treeline, which constitutes one of the World's most conspicuous vegetation limits, remains surprisingly little understood. Although it is known that treeline elevation is closely correlated to temperature conditions, especially those in the soil, the physiological limitations of tree growth (as opposed to the growth of herbaceous plants) under low temperature conditions remain unclear (Körner & Paulsen 2004, Hertel & Wesche 2008, Cierjacks et al. 2008, Körner 2012). One of the reasons for this uncertainty is that, especially in tropical mountains with their long history of human habitation, the vast majority of treeline positions are likely to have been depressed by at least several hundred meters and

differ from their original natural state due to logging, cattle grazing, and burning. Remnants of the true treeline that exhibit a natural state are, thus, restricted to highly inaccessible areas that has confounded their study, even though these relict forests provide the most ecologically meaningful results when attempting to decipher what limits tree establishment, growth and survival at these high elevations. On recording the tallest high elevation forests worldwide from pristine sites in the Cordillera Urubamba (Chapter 4), it becomes more difficult to understand why these trees would not reach to much higher elevations than currently observed. Our data suggests that topmost stands must have a very abrupt decrease in height but, so far, all topmost *Polylepis subsericans* forests have been found with trees much larger than 3 m and with no abrupt decrease in height being observed (S.P. Sylvester *unpubl. data*). This, coupled with data on temperature conditions that are much lower than previously documented for treelines (Körner & Paulsen 2004, Körner 2012) implies that *Polylepis* species may have evolved special physiological adaptations to cope with low temperatures and raises questions regarding their potential distribution in the absence of anthropogenic disturbance.

The outcomes of this research make it obvious the benefit of having a good background in taxonomy when performing ecological studies. Taxonomy is too often undervalued or overlooked when undertaking large-scale ecological studies, but effort placed in the correct identification of specimens can lead to extraordinary results such as those shown in this PhD project. Due to a large part of my formal taxonomic training, passion and interest relating to the Poaceae, I was able to discover that many of the dominant grasses in the pristine ecosystems, reported in chapter 3, were species new to science. Through chapter 6, I hope to have improved the possibilities for correct taxonomic delimitation of *Poa* species by taxonomists working in Peru. I am currently collaborating with Juan Camilo Ospina Gonzalez on taxonomic treatments for *Festuca* from Latin America, which include the new species found dominant in the pristine sites. The grass genus *Deyeuxia*, another dominant component of puna grasslands, is also in need of a thorough taxonomic revision, and with my discovery of two more species, it is high on my list of jobs to do.

Although arduous herbarium work, combined with the help of specialists, allowed the discovery of many rare or undescribed taxa and production of taxonomic treatments to a number of plant groups (eg. Chapters 6 to 10), it was obvious that there are certain taxonomic groups of the Peruvian flora that remain neglected. The best example would be the Asteraceae tribe Senecioneae, a highly diverse group with many species found in the puna biome, but which still lacks a taxonomic treatment for Peru. This monumental task would prove invaluable for ecologists working in Peru and I sincerely hope there is somebody out there brave enough to attempt it. Many other plant groups need similar treatment and it will only be through detailed ecological and taxonomic work, exemplified by this PhD project, that a better understanding of the Peruvian high Andean flora will be achieved.

Accessing remote sites in the Peruvian Andes allowed us to make a number of spectacular discoveries ranging from the realm of ecological inferences (Chapters 1-4), to documentation of new world records and undescribed species (Chapters 4-10). This highlights the advantages of conducting research in unexplored and difficult-to-access areas, despite how physically taxing this may be, as ecologists and taxonomists alike will invariably be rewarded by encountering a whole variety of interesting things to fascinate the world. Unfortunately, more and more research nowadays involves very little fieldwork with

ecologists effectively disconnected from nature, which, at least in my case, was the whole reason to begin a career in ecology. I hope that this thesis may inspire the next generation of ecologists and taxonomists to realise that there is still scope for adventure and excitement when conducting research and that this is not just a thing of the past restricted to the fascinating stories of 18th and 19th century explorers.

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EDUCATION

09/2010-06/2015 **University of Zurich, Switzerland**
PhD project 'Reconstructing the potential natural vegetation of the high Andean puna''.
Ecological study comparing ecosystems with different levels of anthropogenic disturbance in the Cusco region of Peru.

09/2008-09/2009 **University of Edinburgh**
MSc Biodiversity & Taxonomy of Plants- **Distinction**
Summer Project: 'Identification keys to the grass genera of Belize'. Gained experience in key building, expedition planning and identification of neotropical grasses.

09/2002-06/2006 **University of Wales, Bangor & Oregon State University, USA**
BSc Ecology (Hons)-**First class**
Final Year Project: 'Geographic variation in colour pattern and hue of Caribbean lizard *Anolis roquet.'* Used various statistical programs to support hypotheses over the various causes of colour variation.

09/2000-06/2002 **Thomas Rotherham College, South Yorkshire**
'A2' levels- Biology-**A,** Chemistry-**A,** Geography-**A,** General Studies-**C**; 'AS' Environmental Science-**A**, Key Skills-**A**.

09/1996-06/2000 **Notre Dame High School, Sheffield**
GCSE's- 11 subjects A-C including Double Science **A*A*,** Geography **A*,** History **A*,** Religious Education **A*,** English Lit. **A**, English **B**, Maths **B**, German **C.**

WORK / FIELD EXPERIENCE

08/2014-10/2014 **Peruvian Andes. *Project Leader,*** *University of Zurich* - Coordinating and undertaking research on high elevation treelines in remote areas of the southern Peruvian Andes.

08/2010-08/2013 **Peruvian Andes. *Project Leader,*** *University of Zurich* - Coordinating and undertaking botanical field expeditions to remote areas of the southern Peruvian Andes to collect ecological data and plant specimens.

11/2009-04/2010 **Mindo, Ecuador. *Reserve Manager*,** *LifeNet* - Overseeing the general running of a cloudforest reserve including fundraising, implementing research programs (eg. creation of a checklist to the reserves plants and bird surveys) and supervising volunteers in these programs.

05/2008-08/2008 **Lincolnshire, UK. *Head Researcher*,** *University of Leeds* - Leader of team of researchers undertaking farmland plant surveys using quadrats and bird surveys using the breeding bird survey and point count techniques.

03/2007-05/2008 **Sheffield, UK. *Volunteer Ecology Assistant,*** *Sheffield Wildlife Trust* - Gained skills in Phase 1 surveying, NVC and general botanical surveys, GIS mapping using Mapinfo, data input onto Recorder 6, writing of ecological reports, floral identification, bat surveying, small mammal trapping etc. Given responsibility of leading groups on various projects including small mammal trapping, otter surveys and river corridor mapping.

07/2006-08/2006 **Cyprus. *Research assistant*,** *Akrotiri Environmental Centre* - Worked in a group on a number of projects including preparing a proposal for a new nature trail as well as GIS mapping the endangered sea daffodil using Arcview3.2.

09/2004-01/2005 **Ecuador. *Field Assistant*,** *World Wildlife Foundation* - Helped a graduate student with her project on giant river otters as well as carrying out my own research on a project relating water chemistry to the flood pulse concept.

PUBLICATIONS

In peer reviewed journals:

Sundue M, **Sylvester SP**, Kessler M, Lyons B, Ranker TA, Morden CW (accepted) A new species of *Moranopteris* (Polypodiaceae) from inaccessible ledges in the high Andes of Peru. *Systematic Botany*.

Heitkamp F, **Sylvester SP**, Kessler M, Sylvester MDPV, Jungkunst HF (2014) Inaccessible Andean sites reveal human induced weathering in grazed soils. *Progress in Physical Geography* 38(5):576–601.

Kessler M, Toivonen JM, **Sylvester SP**, Kluge J, Hertel D (2014) Elevational patterns of *Polylepis* tree height (Rosaceae) in the high Andes of Peru: role of human impact and climatic conditions. *Frontiers in Functional Plant Ecology.* DOI: 10.3389/fpls.2014.00194.

Sylvester SP (2014**)** *Bartsia lydiae*, a new species of *Bartsia* sect. Laxae (Orobanchaceae) from the southern Peruvian Andes with a revised key to *Bartsia* sect. Laxae. *Phytotaxa* 164 (1): 041–046.

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Sylvester SP, Sylvester, MDPV, Kessler M (2014) Inaccessible ledges as refuges for the natural vegetation of the high Andes. *Journal of Vegetation Science*. DOI: 10.1111/jvs.12176

Submitted:

Sylvester SP, Quandt D, Ammann L, Kessler M (submitted) The World's smallest dicot: *Lysipomia mitsii* sp.nov. *Taxon.*

In preparation (*existing manuscripts, submission imminent*):

Sylvester SP, Heitkamp F, Sylvester MDPV, Jungkunst HF, Sipman HJM, Toivonen JM, Gonzales Inca C, Ospina González JC, Kessler M (in prep.) Shifting perspectives on what is natural! To be submitted to: *Science.*

Sylvester SP, Soreng RJ, Peterson PM (in prep.) An updated checklist and key to the open-panicled *Poa*'s (Poaceae) of Peru including 3 new species, *Poa ramoniana*, *Poa tayacajaensis* and *Poa urubambensis.* To be submitted to: *Phytokeys.*

Ospina González JC**, Sylvester SP**, Sylvester MDPV (in prep.) Taxonomic delimitation of the '*Festuca setifolia'* complex (Poaceae) in southern South America and a new species for the Peruvian Andes. To be submitted to: *Systematic Botany*.

Ospina González JC, **Sylvester SP**, Sylvester MDPV (in prep.) A new species of *Festuca* (Poaceae) from the Peruvian Andes, with redefinition of *Festuca humilior.* To be submitted to: *Phytotaxa.*

Pfanzelt S, **Sylvester SP,** Ammann L (in prep.) *Gentianella viridiflora* (Gentianaceae), a new green-flowered *Gentianella* species from the Peruvian Andes. To be submitted to: *Phytotaxa.*

In preparation (*data collected, preliminary analysis done*):

Sylvester SP, Barrie F (in prep.**)** *Valeriana vilcabambensis*, a new species of *Valeriana* (Caprifoliaceae) from the southern Peruvian Andes**.** To be submitted to: *Phytotaxa***.**

Sylvester SP (in prep.) A new species of *Stellaria* (Caryophyllaceae) from the southern Peruvian Andes. To be submitted to: *Novon.*

Hind N, **Sylvester SP** (in prep.) A new species of *Senecio* (sect. Crassicephali: Asteraceae) from pristine vegetation of the southern Peruvian Andes. To be submitted to: *Phytotaxa*

Kessler M, **Sylvester SP**, Toivonen J, Baiker J, Huggel C, Neukom R, Hertel D (in prep.) Why the World's highest forests are too low. To be submitted to: *Ecology letters*.

Sylvester MDPV, Sipman H, **Sylvester SP**, Kessler M, Toivonen J, Gradstein R, Saji-Saire M, Churchill S (in prep.) The importance of standing deadwood trees of *Polylepis* forests in the high Andes- A case study of lichens. To be submitted to: *Biodiversity and Conservation*.

JOURNAL REVIEWER:

- *Biotropica*

INVITED SPEAKER:

Sylvester SP, Searching for natural vegetation in the high Andes, 10th February 2013- Colloquium- Botanischer Garten und Botanisches Museum Berlin-Dahlem, Germany.

Sylvester SP, The amazing diversity of the grasses (La diversidad asombrosa de los pastos), 15th August 2011, Universidad Nacional del San Antonio Abad del Cusco, Peru.

TEACHING EXPERIENCE:

Universidad Nacional del San Antonio Abad del Cusco, Peru:

09/2011 Planning and conducting a grass identification course for BSc students.

University of Zurich, Switzerland:

03-05/2014 Teaching-Assistant: Practical Course on Biogeography
04-06/2014 Teaching-Assistant: Course on Plant Radiations
03-05/2015 Teaching-Assistant: Practical Course on Biogeography

STUDENT SUPERVISION:

Lolita Ammann	M.Sc. student. University of Zurich. Supervision of thesis writing.
Marisol Saji Saire	Licenciatura. Universidad Nacional del San Antonio Abad del Cusco, Peru. Supervised entire project related to assessing bryophyte diversity and composition in high Andean *Polylepis* forests.
Mitsy Diaz P.V.	Licenciatura. Universidad Nacional del San Antonio Abad del Cusco, Peru. Supervised entire project related to highlighting the importance of standing deadwood in high Andean *Polylepis* forests for increasing lichen diversity in this habitat.

PUBLIC OUTREACH:

20 Minuten- Ein Schädelbruch machte ihn zum Forscher- Swiss newspaper article (12.12.2014). Available at: **http://www.20min.ch/wissen/news/story/Ein-Schaedelbruch-machte-ihn-zum-Forscher-16968109**

UZH News- Mitsii, die kleinste Pflanze der Welt- newspaper article (10.11.2014). Available at: **http://www.uzh.ch/news/articles/2014/mit-der-kletterausruestung-auf-pflanzensuche.html**

Logo - Das Wissenschaftsmagazin. Radio interview (01.02.2014: 21:05) Available at: http://www.ndr.de/info/sendungen/logo_das_wissenschaftsmagazin/

Green Radio - Artenvielfalt: Einfluss des Menschen ist größer und positiver als gedacht (30.01.2014). Available at: **http://detektor.fm/kultur/green-radio-artenvielfalt-einfluss-des-menschen-ist-groesser-und-positiver-**

University of Landau - Press release (08.01.2014). Available at: http://idw-online.de/de/news568254

National Geographic- Deutschland. “Botanik - Aufstieg in eine vergessene Welt” (December 2013 issue). Available at: http://www.nationalgeographic.de/aktuelles/meldungen/botanik-aufstieg-in-eine-vergessene-welt

Public presentation- Zurich botanic garden. “Discovering the natural vegetation of the high Andes” (8.11.2013).

PROFESSIONAL QUALIFICATIONS

Qualification Title	Awarding Body	Date of Award
Certificate in Practical Field Botany	Royal Botanic Garden Edinburgh	01/2009
Plant Classification and Taxonomy	University of Sheffield Institute for Lifelong Learning- obtained through examination	Study 02/2008-04/2008 Award 08/2008
Identification of the Lower Plants	University of Aberystwyth Institute for Lifelong Learning- obtained through examination	Study 28/03/08-30/03/08 Award 06/2008
Level 3 Intro to Mapinfo 7.5	NOCN -obtained through coursework	Training 21/01/08-15/02/08 Award 07/2008
Brushcutters/ Trimmers-Maint. & Operation	LANTRA –obtained through examination	08/2007
Level 2 Intro to Aquatic Fauna ID & Survey Techniques (3 credits)	NOCN -obtained through coursework	08/2007
Level 2 Intro to Flora ID & Survey Techniques (6 credits)	NOCN -obtained through coursework	06/2007
First Aid At Work	HSE –obtained through examination	29/02/07
Level 2 Intro to Habitat Management & Legislation (3 credits)	NOCN -obtained through coursework	02/2007

OTHER PROFESSIONAL DEVELOPMENT TRAINING

TRAINING ESTABLISHMENT	COURSE ATTENDED	FROM	TO
Vogelwarte.ch	Intro to Bayesian ecological analysis Bayesian population analysis with WinBUGS	07/1/2015 07/1/2014	12/1/2015 12/1/2014
Missouri Botanical Garden	Ecological analysis in R	03/10/2012	05/10/2012
Field Studies Council	Introduction to mosses and liverworts BTO Bird Survey & Bird Atlas Techniques Grasses & Sedges Course Fern Course	01/03/08 15/03/08 18/06/08 01/07/08	03/03/08 17/03/08 21/06/08 04/07/08
Shared Earth Trust	Environmental Impact Assessment	21/11/07	23/11/07
Sheffield Wildlife Trust	Badger surveying Fungi course	08/03/08 26/10/07	
Thornbridge Outdoor Centre	MLTE Single Pitch Climbing Instructor Training	22/09/07	23/09/07

COMPETETIVE GRANTS

2014 – G. & A. Claraz-Schenkung, CHF 2,750: fieldwork grant, Andean treeline research.

2013 – University of Zurich Forschungskredit, CHF 82,800: 18 month PhD scholarship.

2010 – Leverhulme Trust, £58,000: PhD studentship.

2009 – Davis Expedition Fund, £1,300: fieldwork grant, 'Identification keys to the grass genera of Belize'.

2008 – NERC, £15,000: MSc scholarship.

AWARDS

Academic: -2009 University of Edinburgh MSc Top Student award
-2002 Foundation Scholarship for academic achievement
-2002 J C Garton Prize for academic achievement

Sport: -2014 Peruvian National Bouldering Championship- 3rd place
-2012 Peruvian National Bouldering Championship- 4th place
-2011 Callalli International Rock Climbing Championship- 2nd place
-2009 Cusco International Rock Climbing Championship- 1st place
-2004 Oregon State University Mountaineering Award
-1998 Duke of Edinburgh Bronze Award